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The Great Basin Naturalist

VOLUME 41, 1981

EDITOR: STEPHEN L. WOOD



PUBLISHED AT BRIGHAM YOUNG UNIVERSITY, BY
BRIGHAM YOUNG UNIVERSITY

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THE GREAT BASIN NATURALIST

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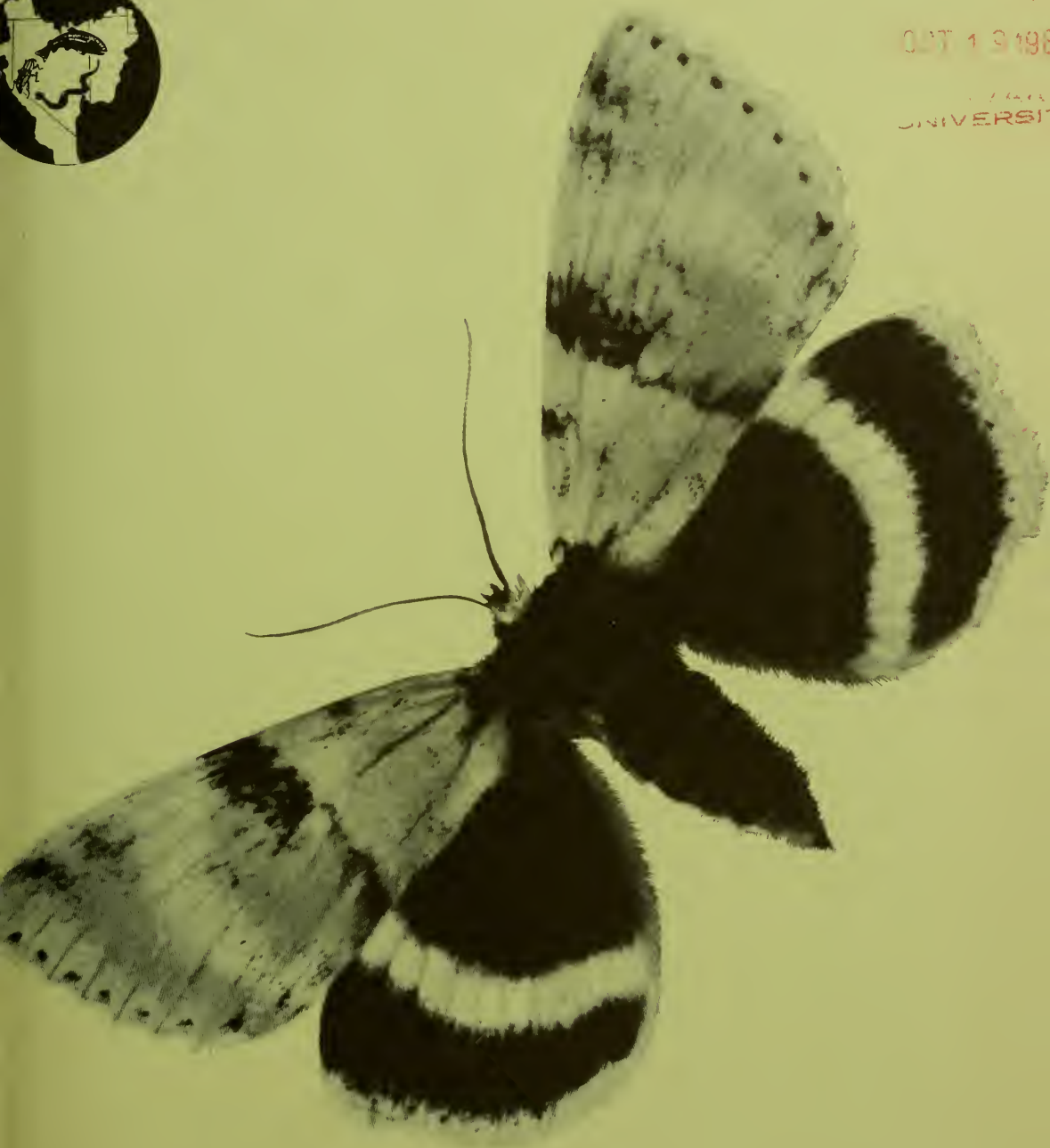
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GREAT BASIN NATURALIST

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Subscriptions. The annual subscription to the *Great Basin Naturalist* is \$12 (outside the United States \$13). The price for single numbers is \$4 each. All back numbers are in print and are available for sale. All matters pertaining to the purchase of subscriptions and back numbers should be directed to Brigham Young University, Life Science Museum, Provo, Utah 84602. The *Great Basin Naturalist Memoirs* may be purchased from the same office at the rate indicated on the inside of the back cover of either journal.

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The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 41

March 31, 1981

No. 1

PRELIMINARY INDEX OF UTAH VASCULAR PLANT NAMES

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ABSTRACT.— Presented herein is an index to vascular plant names of Utah. The names are arranged in alphabetical order by genus, species, and infraspecific taxa. Each entry is followed by a bibliographic citation, family name, rarity (whether endemic, rare, or endemic-rare), and origin (whether indigenous, adventive, or adventive-cultivated). Pertinent synonyms are cited beneath appropriate entries. An index of synonyms and a comprehensive bibliography are included.

For many years there has existed a gap in the plant taxonomy of Utah—no single treatment has included the names of all plant species known for the state. A solution to this difficulty was only partially realized by use of the work by Holmgren and Reveal (1966), which included plant names for the Intermountain Region. Nomenclatural changes and new taxa published since 1966 were not summarized in any publication.

Identification of plants from Utah requires a stack of manuals, floras, and taxonomic revisions to assure inclusion of authors' names, and to provide verification of determinations.

Specimens representing disjunctions in distribution have accumulated in the herbaria of the state. These are well known in many instances, but others have remained obscure. Research leading to the present list of Utah plants has yielded many taxa not previously cited in publications of botany of the state. Thus, herbaria form a principal basis for inclusion of names within the list. The remaining names have been taken from literature (see bibliography).

A list of names and authors alone would have been useful, but bibliographic citations given for the plant names provide an extra tool in evaluation of priority and historical perspective.

Many names of American plants are based on Utah types. A large number of these types represent synonyms, but many are recognized at some taxonomic level in contemporary treatments. Utah type information will be published in a subsequent paper.

Categories of information listed include generic, specific, and infraspecific epithets, author, bibliographic citation, rarity (rare, endemic, rare-endemic), and origin (indigenous, adventive, adventive-cultivated). Synonyms are included in appropriate citations, especially those based on Utah types, but they are not treated as separate citations. An index to pertinent synonyms is appended.

Rarity is a concept involving paucity of collection as much as a concept of actual paucity in numbers or in distributional extent. Plants judged to be rare are those narrowly restricted endemic species as well as

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those of disjunct distributions at the margin of their ranges. Endemics have been cited whether rare or not, because they represent a unique portion of our flora. The endemics are the crown jewels of our state, a part of the natural heritage in unique living things. However, not all of those cited as endemics are restricted entirely within the boundaries of Utah. Where natural physiographic units overlap political boundaries, and the large extent of the known distribution is in Utah, plant taxa which extend beyond the state limits are included in the endemic category (i.e., they are endemic to the natural features that are crossed by political boundaries).

Considerations of endangered or threatened status are beyond the scope of this work. Those concepts are defined in law, and are subject to interpretation. Designations of endangered and threatened categories change more readily than do rarity status categories considered herein. The species listed for status under stipulations of the Endangered Species Act of 1973 (as amended 1978) are contained herein, but are not segregated in any way from among the rare species.

Indigenous plants are those native species that occur naturally within the state. Judgment of which are indigenous is sometimes clouded by lack of information about early introductions in the region. Tentative judgments are followed by a question mark. The same is true for adventive species, those which represent inadvertent introductions from other places, especially from the Old World. Cultivated plants are mainly introductions, and no attempt has been made to provide an exhaustive list of all plants in this category. Some cultivated plants are naturalized and are a part of the continuing flora of the region (i.e., *Ulmus pumila*, *Catalpa speciosa*, *Ligustrum vulgare*, *Robinia pseudoacacia*, and many others). Others are continuously reintroduced, especially weedy species and those grown as crop plants. Additional ones are known only in greenhouse culture, often as mere curiosities. In any event, cultivated plants seldom are collected. We have listed, mainly, those represented in herbaria and have not distinguished among naturalized and reintroduced species or the greenhouse curiosities. That work will await

future listing and represents an area of study by itself.

Taxonomic literature has been checked for most citations, but is by no means exhaustive. Dates were missing for many bibliographic citations, especially for those of cultivated plants. Dates are not included in Index Kewensis, and many of the citations given in it are incorrect for these early named Old World introductions. Completion of citation is based on review of other literature, especially from *Taxonomic Literature* (Stafleu, F. A. 1967. Regnum Vegetabile. Vol. 57.). An attempt has been made to standardize literature citation and author abbreviations, but additional work is needed. All standard library references have been consulted, including the *Union List of Serials* and the *Catalogue of the British Museum*.

It is expected that this preliminary list will be expanded and improved by inclusion of data from other herbaria in Utah, whose curators are invited to participate in updating and in coauthoring a subsequent revision.

Almost 5200 names were programmed into the computer. A query of this information yielded the following preliminary data on indigenous, cultivated, and adventive taxa within Utah. These are the names included in the following checklist:

	Species	Subspecies and varieties	Total
Indigenous	2575	325	2900
Cultivated	371	4	375
Adventive	325		325
Total Utah flora	3271	329	3600

These figures should not be taken as final, because of the preliminary nature of the listing.

A copy of the complete computer printout of names is available from the herbarium of Brigham Young University upon request.

The authors of this list wish to acknowledge and to thank those who have aided in the laborious research involved in this undertaking. They have made possible the checking and double-checking that has transformed the first rough list into a work of some thoroughness. They have sought out obscure bibliographic citations, and the uniformity is a tribute to their diligence. Help was given by

Matthew Chatterley, Deborah Engle, Trudy Fjeldsted, Robert Jeppsen, Blaine Welsh, and Alan Taye.

Indigenous, Adventive, and Cultivated Utah Plants (18-FEB-81)

- Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., Verbr. Conif. 261. 1861. Pinaceae. Indigenous.
- Abies lasiocarpa* (Hook.) Nutt., N. Amer. Sylva 3: 138. 1849. Pinaceae. Indigenous.
- Abronia argillosa* Welsh & Goodrich, Great Basin Nat. 40: 78. 1980. Nyctaginaceae. Indigenous.
- Abronia elliptica* A. Nels., Bull. Torrey Bot. Club 26: 7. 1899. Nyctaginaceae. Indigenous. Syn: *A. fallax* Heimerl; *A. fragrans* var. *pterocarpa* Jones; *A. pumila* Rydb.; *A. salsa* Rydb.
- Abronia fragrans* Nutt. ex Hook., J. Bot. & Kew Miscell. 5: 261. 1853. Nyctaginaceae. Indigenous.
- Abronia mellifera* Dougl. ex Hook., Bot. Mag. 56: 2879. 1829. Nyctaginaceae. Indigenous.
- Abronia nana* Wats., Proc. Amer. Acad. 14: 294. 1879. Nyctaginaceae. Indigenous.
- Abronia villosa* Wats., Amer. Naturalist 7: 307. 1873. Nyctaginaceae. Indigenous.
- Abutilon incanum* (Link) Sweet, Hort. Brit. 533. 1826. Malvaceae. Indigenous.
- Abutilon parvulum* Gray, Pl. Wright. 1: 21. 1852. Malvaceae. Indigenous.
- Abutilon pictum* Walp., Repert. Bot. Syst. 1: 324. 1842. Malvaceae. Adventive; cultivated.
- Abutilon theophrasti* Medic., Kunstl. Geschl. Malv.-Fam. 28. 1787. Malvaceae. Adventive.
- Acacia greggii* Gray, Pl. Wright. 1: 65. 1852. Fabaceae. Indigenous. Rare.
- Acampopappus sphaerocephalus* (Harv. & Gray) Gray, Proc. Amer. Acad. 8: 634. 1874. Asteraceae. Indigenous.
- Acanthochiton wrightii* Torr. in Sitgr., Rep. Zuni & Colorado Riv. 170. 1853. Amaranthaceae. Indigenous.
- Acer campestre* L., Sp. Pl. 1055. 1753. Aceraceae. Adventive; cultivated.
- Acer circinatum* Pursh, Fl. Amer. Sept. 1: 267. 1814. Aceraceae. Adventive; cultivated.
- Acer ginnale* Maxim., Bull. Phys.-Math. Acad. (Petersb.) 15: 126. 1856. Aceraceae. Adventive; cultivated.
- Acer glabrum* Torr., Ann. Lyceum Nat. Hist. New York 2: 172. 1828. Aceraceae. Indigenous.
- Acer grandidentatum* Nutt. in T. & G., Fl. N. Amer. 1: 247. 1838. Aceraceae. Indigenous.
- Acer negundo* L., Sp. Pl. 1056. 1753. Aceraceae. Adventive; cultivated.
- Acer negundo* L. var. *interius* (Britt.) Sarg., Bot. Gaz. 67: 239. 1919. Aceraceae. Indigenous.
- Acer palmatum* Thunb., Fl. Jap. 162. 1784. Aceraceae. Adventive; cultivated.
- Acer platanoides* L., Sp. Pl. 1055. 1753. Aceraceae. Adventive; cultivated.
- Acer pseudoplatanus* L., Sp. Pl. 1054. 1753. Aceraceae. Adventive; cultivated.
- Acer rubrum* L., Sp. Pl. 1055. 1753. Aceraceae. Adventive; cultivated.
- Acer saccharinum* L., Sp. Pl. 1055. 1753. Aceraceae. Adventive; cultivated.
- Acer saccharum* Marsh., Arbust. Amer. 4. 1785. Aceraceae. Adventive; cultivated.
- Achillea filipendulina* Lam., Encycl. Meth. Bot. 1: 27. 1783. Asteraceae. Adventive; cultivated.
- Achillea millefolium* L. ssp. *lanulosa* (Nutt.) Piper, Mazama 2: 97. 1901. Asteraceae. Indigenous.
- Achillea millefolium* L. ssp. *millefolium*, Sp. Pl. 899. 1753. Asteraceae. Adventive; cultivated.
- Achyronichia cooperi* T. & G., Proc. Amer. Acad. 7: 331. 1868. Caryophyllaceae. Indigenous. Rare.
- Aconitum columbianum* Nutt. in T. & G., Fl. N. Amer. 1: 34. 1838. Ranunculaceae. Indigenous. Syn: *A. divaricatum* Rydb.; *A. glaberrimum* Rydb.
- Actaea rubra* (Ait.) Willd., Hort. Berol. 561. 1809. Ranunculaceae. Indigenous.
- Adiantum capillus-veneris* L. var. *modestum* (Underw.) Fern., Rhodora 52: 206. 1950. Pteridaceae. Indigenous. Syn: *A. modestum* Underw.
- Adiantum capillus-veneris* L. var. *modestum* f. *rimicola* (Slosson) Fern., Rhodora 52: 208. 1950. Pteridaceae. Indigenous. Syn: *A. rimicola* Slosson.
- Adiantum capillus-veneris* L. var. *protrusum* Fern., Rhodora 52: 203. 1950. Polypodiaceae. Indigenous.
- Adiantum pedatum* L., Sp. Pl. 1095. 1753. Polypodiaceae. Indigenous.
- Adonis aestivalis* L., Sp. Pl. ed. 2. 771. 1763. Ranunculaceae. Adventive. Syn: *A. annua* L.
- Adoxa moschatellina* L., Sp. Pl. 367. 1753. Adoxaceae. Indigenous.
- Aegilops cylindrica* Host, Icon. Descr. 2: 6. 1802. Poaceae. Adventive.
- Aegopodium podagraria* L., Sp. Pl. 265. 1753. Poaceae. Adventive; cultivated.
- Aesculus carnea* Hayne in Guimpel, Otto, & Hayne, Abbild. Fremd. Holzart. 25. 1825. Hippocastanaceae. Adventive; cultivated.
- Aesculus glabra* Willd., Enum. Pl. Hort. Berol. 405. 1809. Hippocastanaceae. Adventive; cultivated.
- Aesculus hippocastanum* L., Sp. Pl. 344. 1753. Hippocastanaceae. Adventive; cultivated.
- Aesculus octandra* Marsh., Arbust. Amer. 4. 1785. Hippocastanaceae. Adventive; cultivated.
- Agastache urticifolia* (Benth.) Kuntze, Rev. Gen. 2: 511. 1891. Lamiaceae. Indigenous. Syn: *Lophanthus urticifolia* Benth.
- Agave utahensis* Engelm. in Wats. var. *utahensis* Rep., U.S. Geol. Explor. 40th Parallel, Bot. 5: 497. 1871. Agavaceae. Indigenous.
- Agoseris aurantiaca* (Hook.) Greene, Pittonia 2: 177. 1891. Asteraceae. Indigenous. Syn: *Troximon aurantiacum* Hook.
- Agoseris elata* (Nutt.) Greene, Pittonia 2: 177. 1891. Asteraceae. Indigenous.
- Agoseris glauca* (Pursh) Raf., Herb. Rafin. Atl. J.2: 39. 1833. Asteraceae. Indigenous. Syn: *Troximon glaucum* Pursh.
- Agoseris grandiflora* (Gray) Greene, Pittonia 2: 178. 1891. Asteraceae. Indigenous. Syn: *Troximon grandiflorum* Gray.
- Agoseris heterophylla* (Nutt.) Greene, Pittonia 2: 178. 1891. Asteraceae. Indigenous. Syn: *Macrorhynchus heterophyllus* Nutt.
- Agrohordeum macounii* (Vasey) Lepage, Naturaliste Canad. 79: 242. 1952. Poaceae. Indigenous.

- Agropyron cristatum* (L.) Gaertn., *Novi Comment. Acad. Sci. Petrop.* 14: 540. 1770. Poaceae. Adventive.
- Agropyron dasystachyum* (Hook.) Scribn., *Bull. Torrey Bot. Club.* 10: 78. 1883. Poaceae. Indigenous. Syn: *A. albicans* Scribn. & Sm.
- Agropyron elongatum* (Host) Beauv., *Essai Nouv. Agrostogr.* 102, 146, 180. 1812. Poaceae. Adventive.
- Agropyron intermedium* (Host) Beauv., *Essai Nouv. Agrostogr.* 102, 146, 180. 1812. Poaceae. Adventive.
- Agropyron intermedium* (Host) Beauv. var. *trichophorum* (Link) Halacsy, *Consp. Fl. Graec.* 3: 437. 1904. Poaceae. Adventive.
- Agropyron pseudorepens* Scribn. & Sm., (Hybrid) USDA Div. Agrostol. Bull. 4:34. 1897. Poaceae. Indigenous.
- Agropyron pseudorepens* Scribn. & Sm., USDA Div. Agrostol. Bull. 4: 34. 1897. Poaceae. Indigenous.
- Agropyron repens* (L.) Beauv., *Sp. Pl.* 86. 1753. Poaceae. Adventive.
- Agropyron scribneri* Vasey, *Bull. Torrey Bot. Club* 10: 128. 1883. Poaceae. Indigenous.
- Agropyron smithii* Rydb., *Mem. New York Bot. Gard.* 1: 64. 1900. Poaceae. Indigenous.
- Agropyron spicatum* (Pursh) Scribn. & Sm., USDA Div. Agrostol. Bull. 4: 33. 1897. Poaceae. Indigenous.
- Agropyron trachycaulum* (Link) Malte, *Annual Rep. Natl. Mus. Canad.* 1930: 42. 1932. Poaceae. Indigenous.
- Agropyron triticeum* Gaertn., *Nov. Comment Acad. Sci. Petrop.* 14(1): 540. 1770. Poaceae. Adventive. Syn: *Eremopyrum triticeum* (Gaertn.) Nevski.
- Agrostitanion saundersii* (Vasey) Bowden, *Canad. J. Bot.* 45: 720. 1967. Poaceae. Indigenous. Syn: *Agropyron saundersii* Vasey.
- Agrostitanion saxicola* (Scribn.) Bowden, *Canad. J. Bot.* 45: 711. 1967. Poaceae. Indigenous. Syn: *Sitanion insulare* J. G. Sm.; *Agropyron saxicola* (Scribn. & Sm.) Piper; *Elymus saxicolus* Scribn. & Sm.
- Agrostis borealis* Hartman, *Handb. Skand. Fl.* ed. 3: 17. 1838. Poaceae. Indigenous?
- Agrostis exarata* Trin., *Gram. Unifloris & Sesquifloris* 209. 1824. Poaceae. Indigenous.
- Agrostis humilis* Vasey, *Bull. Torrey Bot. Club* 10: 21. 1883. Poaceae. Indigenous.
- Agrostis idahoensis* Nash, *Bull. Torrey Bot. Club* 24: 42. 1892. Poaceae. Indigenous.
- Agrostis scabra* Willd., *Sp. Pl.* 1: 370. 1797. Poaceae. Indigenous. Syn: *A. hymenalis* (Walt.) B.S.P.
- Agrostis stolonifera* L. var. *palustris* (Huds.) Farw., *Annual Rep. Michigan Acad. Sci.* 21: 351. 1920. Poaceae. Indigenous.
- Agrostis stolonifera* L. var. *stolonifera*, *Sp. Pl.* 62. 1753. Poaceae. Indigenous. Syn: *A. alba* L.
- Agrostis tenuis* Sibth., *Fl. Oxon.* 36. 1794. Poaceae. Indigenous.
- Agrostis thurberiana* A.S. Hitchc., *USDA Bur. Pl. Industr. Bull.* 68: 23. 1905. Poaceae. Indigenous.
- Agrostis variabilis* Rydb., *Mem. New York Bot. Gard.* 1: 37. 1900. Poaceae. Indigenous. Syn: *A. rossiae* Vasey.
- Ailanthus altissima* (Mill.) Swingle, *J. Washington Acad. Sci.* 6: 495. 1916. Simarubaceae. Adventive; cultivated.
- Ajuga reptans* L., *Sp. Pl.* 561. 1753. Lamiaceae. Adventive; cultivated.
- Albizia julibrissin* Durazz., *Mag. Tosc.* 4: 11. 1772. Fabaceae. Adventive; cultivated.
- Aletes macdougallii* Coult. & Rose ssp. *treviaristatus* Theobald & Tseng, *Brittonia* 16: 306. 1964. Apiaceae. Indigenous.
- Alisma gramineum* Lej., *Fl. Spa* 175. 1811. Alismataceae. Indigenous. Syn: *A. geyeri* Torr.
- Alisma plantago-aquatica* L., *Sp. Pl.* 347. 1753. Alismataceae. Indigenous. Syn: *A. triviale* Pursh; *A. subcordatum* Raf.
- Allenrolfea occidentalis* (Wats.) Kuntze, *Rev. Gen.* 2: 546. 1891. Chenopodiaceae. Indigenous. Syn: *Halostachys occidentalis* Wats.
- Allionia incarnata* L., *Syst. Nat.* ed. 10. 2: 890. 1759. Nyctaginaceae. Indigenous.
- Allium acuminatum* Hook., *Fl. Bor.-Amer.* 2: 184. 1838. Liliaceae. Indigenous.
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- Convallaria majalis* L., Sp. Pl. 314. 1753. Liliaceae. Adventive; cultivated.
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- Corispermum nitidum* Kit. in Schult., Oestereichs Fl. ed. 2. 1: 7. 1814. Chenopodiaceae. Adventive.
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Index of Utah Plant Synonyms

- Abies subalpina* Engelm. ex Ward
= *A. lasiocarpa* (Hook.) Nutt.
Abronia fallax Heimerl ex Rydb.
= *A. elliptica* A. Nels.
Abronia fragrans Nutt. ex Hook. var. *pterocarpa* Jones
= *A. elliptica* A. Nels.
Abronia micrantha Torr. var. *pedunculata* Jones
= *Tripterocalyx micrantha* (Torr.) Hook.
Abronia pumila Rydb.
= *A. elliptica* A. Nels.
Abronia salsa Rydb.
= *A. elliptica* A. Nels.
Abronia turbinata var. *marginata* Eastw.
= *A. fragrans* Nutt.
Acerates decumbens var. *erecta* Durand
= *Asclepias asperula* (Decne.) Woodson
Acer kingii Britt. in Britt. & Shafer
= *A. negundo* var. *interius* (Britt.) Sarg.
Acer negundo L. ssp. *interius* (Britt.) Love & Love
= *A. negundo* var. *interius* (Britt.) Sarg.
Acer saccharum Marsh. ssp. *grandidentatum* (Nutt.)
Desmarais
= *A. grandidentatum* Nutt.
Acer saccharum Marsh. var. *grandidentatum* (Nutt.)
Sudw.
= *A. grandidentatum* Nutt.
Achillea lanulosa Nutt.
= *A. millefolium* ssp. *lanulosa* (Nutt.) Breiteng
Aconitum divaricatum Rydb.
= *A. columbianum* Nutt. in T. & G.
Aconitum glaberrimum Rydb.
= *A. columbianum* Nutt. in T. & G.
Actaea arguta Nutt. ex T. & G.
= *A. rubra* (Ait.) Willd.
Adiantum modestum Underw.
= *A. capillus-veneris* var. *modestum* (Underw.) Fern.
Adiantum rimicola Slosson
= *A. capillus-veneris* var. *modestum* f. *rimicola* (Slosson)
Fern.
Adonis annua L.
= *A. aestivalis* L.
Agave scaphoidea Greenm. & Roush
= *A. utahensis* Engelm. var. *utahensis*
Agoseris arizonica Greene
= *A. aurantiaca* (Hook.) Greene
Agoseris caudata Greene
= *A. glauca* (Pursh) Raf.
Agoseris confinis Greene
= *A. aurantiaca* (Hook.) Greene
Agoseris gracilens (Gray) Kuntze
Syn: *Troximon gracilens* Gray; = *A. aurantiaca* (Hook.)
Greene
Agoseris isomeris Greene
= *A. glauca* (Pursh) Raf.
Agoseris longirostris Greene
= *A. aurantiaca* (Hook.) Greene
Agoseris pumila (Nutt.) Rydb.
Syn: *Troximon pumilum* Nutt. = *A. glauca* (Pursh) Raf.
Agoseris retrorsa (Benth.) Greene
Syn: *Troximon retrorsum* Gray Rep. Err.
Agoseris taraxacifolia (Nutt.) D. Dietr.
= *A. glauca* (Pursh) Raf.
Agoseris taraxacoides Greene
= *A. glauca* (Pursh) Raf.
Agoseris villosa Rydb.
= *A. glauca* (Pursh) Raf.
Agropyron albicans Scribn. & Sm.
= *A. dasystachyum* (Hook.) Scribn.
Agropyron bakeri E. Nels.
= *A. scribneri* Vasey
Agropyron caninum (L.) Beauv. var. *andinum* (Scribn. &
Sm.) Pease & Moore
= *A. trachycaulum* var. *glaucum* (Pease & Moore)
Malte
Agropyron caninum (L.) Beauv. var. *hornemannii* (Koch)
Pease & Moore
= *A. trachycaulum* (Link) Malte
Agropyron caninum (L.) Beauv. var. *latiglume* (Scribn. &
Sm.) Pease & Moore
= *A. trachycaulum* var. *latiglume* (Scribn. & Sm.)
Beetle
Agropyron caninum L. Beauv. ssp. *majus* (Vasey) C.L.
Hitchc.
= *A. trachycaulum* var. *trachycaulum*
Agropyron caninum (L.) Beauv. var. *unilaterale* Vasey
= *A. trachycaulum* var. *unilaterale* (Cassidy) Malte
Agropyron desertorum (Fisch.) Schult. & Schult.
= *A. cristatum* (L.) Gaertn.
Agropyron griffithsii Scribn. & Sm. ex Piper
= *A. albicans* Scribn. & Sm.
Agropyron inerme (Scribn. & Sm.) Rydb.
= *A. spicatum* (Pursh) Scribn. & Sm.
Agropyron latiglume (Scribn. & Sm.) Rydb.
= *A. trachycaulum* var. *latiglume* (Scribn. & Sm.)
Beetle
Agropyron pauciflorum (Schwein.) A.S. Hitchc. ex
Silveus
= *A. trachycaulum* (Link) Malte
Agropyron pseudorepens Scribn. & Sm.
= *A. repens* (L.) Beauv.

- Agropyron riparium* Scribn. & Sm.
 = *A. dasystachyum* (Hook.) Scribn.
- Agropyron saundersii* (Vasey) A.S. Hitchc.
 = *Agrositanion saundersii* (Vasey) Bowden
- Agropyron saxicola* (Scribn. & Sm.) Piper
 = *Agrositanion saxicola* (Scribn. & Sm.) Bowden
- Agropyron subsecundum* (Link) A.S. Hitchc.
 = *A. trachycaulum* var. *unilaterale* (Cassidy) Malte
- Agropyron trichophorum* (Link) Richter
 = *A. intermedium* var. *trichophorum* (Link) Halec.
- Agrostis airoides* Torr.
 = *Sporobolus airoides* (Torr.) Torr.
- Agrostis alba* L.
 = *A. stolonifera* L.
- Agrostis cryptandra* Torr.
 = *Sporobolus cryptandrus* (Torr.) Gray
- Agrostis hiemalis* (Walt.) B.S.P.
 = *A. scabra* Willd.
- Agrostis interrupta* L.
 = *Apera interrupta* (L.) Bailey
- Agrostis latifolia* Trev. ex Gopp.
 = *Cinna latifolia* (Trev.) Gopp.
- Agrostis palustris* Huds.
 = *A. stolonifera* var. *palustris* (Huds.) Farw.
- Agrostis racemosa* Michx.
 = *Muhlenbergia racemosa* (Michx.) B.S.P.
- Agrostis rossae* Vasey
 = *A. variabilis* sensu Utah
- Agrostis semiverticillata* (Forssk.) C. Christensen
 Syn: *A. verticillata* Vell.; = *Polypogon semiverticillata* (Forsk.) Hylander
- Agrostis verticillata* Vell.
 = *A. semiverticillata* (Forssk.) Christensen
- Alcea rosea* L.
 = *Althaea rosea* (L.) Cav.
- Aletes tenuifolia* Coult. & Rose
 = *Musineon lineare* (Rydb.) Mathias
- Alisma geyeri* Torr. in Nicolle
 = *A. gramineum* Lej.
- Alisma subcordatum* Raf.
 = *A. plantago-aquatica* L.
- Alisma triviale* Pursh
 = *A. plantago-aquatica* L.
- Allionia choisyi* Standl.
 Syn: *A. glabra* var. *incarnata* Choisy, not Kuntze
- Allium biceptrum* var. *utahense* Jones
 = *A. biceptrum* var. *biceptrum*
- Allium cristatum* Wats.
 = *A. nevadense* Wats.
- Allium diehlai* (Jones) Jones
 Syn: *A. tribracteatum* var. *diehlai* Jones; = *A. brandegei* Wats.
- Allium nevadense* Wats. var. *cristatum* (Wats.) M. Ownbey
 Syn: *A. cristatum* Wats.; = *A. nevadense* Wats.
- Allium palmeri* Wats.
 = *A. biceptrum* Wats. var. *palmeri* (Wats.) Cronq.
- Allium reticulatum* var. *deserticola* Jones
 = *A. macropetalum* Rydb.
- Allium rubrum* Osterh.
 = *A. geyeri* Wats.
- Allium tribracteatum* Torr. var. *diehlai* Jones
 = *A. brandegei* Wats.
- Allocarya cognata* Greene
 = *Plagiobothrys scouleri* (H. & A.) Johnst.
- Allocarya orthocarpa* Greene
 = *Plagiobothrys leptocladus* (Greene) Johnst.
- Alnus tenuifolia* Nutt.
 = *A. incana* (L.) Moench
- Alsine crispa* Holz.
 = *Stellaria crispa* C. & S.
- Alsine media* L.
 = *Stellaria media* L.
- Alsine palmeri* Rydb.
 = *Stellaria obtusa* Engelm.
- Amauria* (?) *dissecta* Gray
 = *Bahia dissecta* (Gray) Britt.
- Ambrosia coronopifolia* T. & G.
 = *A. psilostachya* DC.
- Ambrosia elatior* L.
 = *A. artemisiifolia* L.
- Amesia gigantea* (Dougl.) Nels. & Macbr.
 = *Epipactis gigantea* Dougl.
- Amsinckia catonii* Suksd.
 = *A. retrorsa* Suksd.
- Amsinckia hispidissima* Suksd.
 = *A. retrorsa* Suksd.
- Amsinckia rugosa* Rydb.
 = *A. retrorsa* Rydb.
- Amsinckia utahensis* Suksd.
 = *A. tessellata* Gray.
- Amsonia brevifolia* Gray
 = *A. jonesii* Woodson
- Amsonia latifolia* Jones
 = *A. jonesii* Woodson
- Andropogon barbinodis* Lag.
 = *Bothriochloa barbinodis* (Lag.) Herter
- Andropogon furcatus* Muhl. in Willd.
 = *A. gerardii* Vitman
- Andropogon saccharoides* Swartz
 = *Bothriochloa barbinodis* (Lag.) Herter
- Andropogon scoparius* Michx.
 = *Schizachyrium scoparium* (Michx.) Nash
- Anemone cylindrica* authors, not Gray
 = *A. multifida* Poir.
- Anemone globosa* Nutt. in Pritz.
 = *A. multifida* Poir.
- Anemone multifida* Poir. var. *tetonensis* (Porter) C.L. Hitchc.
 Syn: *A. tetonensis* Porter; = *A. multifida* Poir.
- Anemone stylosa* A. Nels.
 = *A. multifida* Poir.
- Anemone tetonensis* Porter
 Syn: *A. multifida* var. *tetonensis* (Porter) C. L. Hitchc.
 = *A. multifida* Poir.
- Angelica dilatata* A. Nels. in Coult. & Rose
 = *A. wheeleri* Wats.

- Angelica leporina* Wats.
= *A. pinnata* Wats.
- Anotites jonesii* Greene
= *Silene menziesii* Hook.
- Antennaria aprica* Greene
= *A. parvifolia* Nutt.
- Antennaria arida* E. Nels.
= *A. microphylla* Rydb.
- Antennaria austromontana* E. Nels.
= *A. alpina* var. *media* (Greene) Jeps.
- Antennaria carpathica* var. *pulcherrima* Hook.
= *A. pulcherrima* (Hook.) Greene
- Antennaria concinna* E. Nels.
= *A. microphylla* Rydb.
- Antennaria dimorpha* (Nutt.) T. & G. var. *macrocephala* D.C. Eaton
= *A. dimorpha* (Nutt.) T. & G.
- Antennaria dioica* authors, not (L.) Gaertn.
= *A. umbrinella* Rydb.
- Antennaria marginata* Greene
= *A. neglecta* Greene
- Antennaria media* Greene
= *A. alpina* (L.) Gaertn.
- Antennaria nardina* Greene
= *A. corymbosa* E. Nels.
- Antennaria oblanceolata* Rydb.
= *A. luzuloides* T. & G.
- Antennaria obtusata* Greene
= *A. aprica* Greene
- Antennaria rosea* (D.C. Eaton) Greene
= *A. microphylla* Rydb.
- Anticlea vaginata* Rydb.
= *Zigadenus vaginatus* (Rydb.) Macbr.
- Apocynum convallarium* Greene
= *A. medium* Greene
- Apocynum suksdorfii* Greene
= *A. cannabinum* L.
- Aquilegia caerulea* James var. *calcareae* Jones
= *A. scopulorum* var. *calcareae* (Jones) Munz
- Aquilegia depauperata* Jones
= *A. flavescens* Wats.
- Aquilegia lithophila* Payson
= *A. micrantha* Eastw.
- Aquilegia pallens* Payson
= *A. micrantha* Eastw.
- Aquilegia rubicunda* Tidestr.
= *A. micrantha* Eastw.
- Arabis diehlii* Jones
= *A. pendulina* Greene
- Arabis divaricarpa* A. Nels.
Syn: *A. stokesiae* Rydb. = *A. confinis* Wats.
- Arabis holboellii* Hornem. var. *retrofracta* (Graham) Rydb.
= *A. holboellii* Hornem. var. *secunda* (Howell) Jeps.
- Arabis oreophila* Rydb.
= *A. lyallii* Wats.
- Arabis setulosa* Greene
= *A. pendulina* Greene
- Arabis stokesiae* Rydb.
Syn: *A. divaricarpa* A. Nels.; = *A. confinis* Wats.
- Arabis thalliana* L.
= *Arabidopsis thalliana* (L.) Schur
- Aragallus majusculus* Greene
= *Oxytropis sericea* Nutt.
- Arctostaphylos platyphylla* (Gray) Kuntze
= *A. patula* Greene
- Arenaria calycantha* Ledeb.
= *Stellaria calycantha* (Ledeb.) Bong.
- Arenaria fendleri* (Rydb.) Fern. ssp. *brevifolia* Maguire
= *A. fendleri* var. *brevifolia* (Maguire) Maguire
- Arenaria kingii* (Wats.) Jones ssp. *plateauensis* Maguire
= *A. kingii* var. *plateauensis* (Maguire) Reveal
- Arenaria media* L.
= *Spergularia media* (L.) Presl.
- Arenaria nuttallii* Pax var. *gracilipes* Jones
= *A. nuttallii* Pax
- Arenaria rubra* L.
= *Spergularia rubra* (L.) J. & C. Presl
- Arenaria rubra* L. var. *marina* L.
= *Spergularia marina* (L.) Griseb.
- Arenaria uintahensis* A. Nels.
= *A. kingii* ssp. *uintahensis* (A. Nels.) Maguire
- Argemone rotundata* Rydb.
= *A. munita* ssp. *rotundata* (Rydb.) G.B. Ownbey
- Aristida fendleriana* Steud.
= *A. purpurea* var. *longiseta* (Steud.) Vasey
- Aristida glauca* (Nees) Walp.
= *A. purpurea* var. *glauca* (Nees) A. & N. Holmgren
- Aristida longiseta* Steud.
= *A. purpurea* var. *longiseta* (Steud.) Vasey
- Aristida wrightii* Nash in Small
= *A. purpurea* var. *glauca* (Nees) A. & N. Holmgren
- Arnica arachnoidea* Rydb.
= *A. mollis* Hook.
- Arnica caudata* Rydb.
= *A. longifolia* D.C. Eaton
- Arnica chamissonis* Less. var. *longinodosa* A. Nels.
= *A. mollis* Hook.
- Arnica foliosa* Nutt.
= *A. chamissonis* ssp. *foliosa* (Nutt.) Maguire
- Arnica foliosa* Nutt. var. *incana* Gray
= *A. chamissonis* var. *incana* (Gray) Hulten
- Arnica gracilis* Rydb.
= *A. latifolia* Bong.
- Arnica jonesii* Rydb.
= *A. latifolia* Bong.
- Arnica ovata* Greene
= *A. mollis* Hook.
- Arnica pedunculata* Rydb.
= *A. fulgens* Pursh
- Artemisia aromatica* A. Nels.
= *A. dracunculus* L.
- Artemisia cana* Pursh ssp. *viscidula* (Osterh.) Beetle
= *O. cana* var. *viscidula* Osterh.
- Artemisia discolor* Dougl. ex Bess.
= *A. michauxiana* Bess.

- Artemisia dracunculoides* Pursh
= *A. dracunculus* L.
- Artemisia forwoodii* Wats.
= *A. campestris* L.
- Artemisia gnaphaloides* Nutt.
= *A. ludoviciana* Nutt.
- Artemisia pacifica* Nutt.
= *A. campestris* L. ssp. *pacifica* (Nutt.) H. & C.
- Artemisia spithamea* Pursh
= *A. campestris* L.
- Artemisia tridentata* Nutt. ssp. *arbuscula* (Nutt.) H. & C.
= *A. arbuscula* Nutt.
- Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle
Syn: *A. vaseyana* Rydb.; = *A. tridentata* var. *vaseyana* (Rydb.) B. Boi.
- Artemisia wrightii* Gray
= *A. carruthii* Wood ex Carruth
- Asclepias capricornu* Woodson
= *A. asperula* (Decne) Woodson
- Asclepias galioides* H.B.K.
= *A. subverticillata* (Gray) Vail
- Asclepias involucrata* Engelm. var. *tomentosa* Eastw.
= *A. macrosperma* Eastw.
- Asclepias verticillata* var. *subverticillata* Gray
= *A. subverticillata* (Gray) Vail
- Aspidium aculeatum* var. *scopulinum* D.C. Eaton
= *Polystichum scopulinum* (D.C. Eaton) Maxon
- Astephanus utahensis* Engelm.
= *Cynanchum utahense* (Engelm.) Woodson
- Aster abatus* Blake
= *Machaeranthera tortifolia* (Greene) Cronq. & Keck
- Aster adscendens* Lindl. in DC.
= *A. chilensis* ssp. *adscendens* (Lindl.) Cronq.
- Aster angustus* (Lindl.) T. & G., not Nees
Syn: *Tripolium angustum* Lindl.; = *Aster brachyactis* Blake
- Aster arenarioides* D.C. Eaton in Gray
= *Erigeron arenarioides* (D.C. Eaton) Rydb.
- Aster arenosus* (Heller) Blake
= *Leucelene ericoides* (Torr.) Greene
- Aster bigelovii* Gray
= *Machaeranthera bigelovii* (Gray) Greene
- Aster canescens* Pursh
= *Machaeranthera canescens* (Pursh) Gray
- Aster canescens* Pursh var. *aristatus* Eastw.
= *Machaeranthera canescens* (Pursh) Gray
- Aster cichoriaceus* (Greene) Blake
= *Machaeranthera linearis* Greene
- Aster coerulescens* authors, not DC.
= *A. hesperius* Gray
- Aster commutatus* (T. & G.) Gray
= *A. falcatus* Lindl. in Hook.
- Aster elegans* var. *engelmannii* D.C. Eaton in Wats.
= *A. engelmannii* (D.C. Eaton) Gray
- Aster ericaefolius* Roth ex Coult.
= *Leucelene ericoides* (Torr.) Greene
- Aster foliaceus* var. *eatonii* Gray
= *A. eatonii* (Gray) Howell
- Aster glaucodes* Blake ssp. *pulcher* Blake
= *A. glaucodes* Blake
- Aster glaucus* var. *wasatchensis* Jones
= *A. wasatchensis* (Jones) Blake
- Aster halophilus* Greene
= *A. chilensis* ssp. *adscendens* (Lindl.) Cronq.
- Aster hirtifolius* Blake in Tidestr.
= *Leucelene ericoides* (Torr.) Greene
- Aster kingii* D.C. Eaton in Wats.
= *Machaeranthera kingii* (D.C. Eaton) Cronq. & Keck.
- Aster laetevirens* Greene
= *A. hesperius* Gray
- Aster leucanthemifolius* Greene
= *Machaeranthera leucanthemifolia* (Greene) Greene
- Aster leucopsis* Greene
= *A. chilensis* ssp. *adscendens* (Lindl.) Cronq.
- Aster linearis* (Greene) Cory
= *Machaeranthera linearis* Greene
- Aster multiflorus* var. *pansus* Blake
= *A. pansus* (Blake) Cronq.
- Aster oregonus* (Nutt.) T. & G.
= *A. eatonii* (Gray) Howell
- Aster pansus* (Blake) Cronq.
Syn: *A. multiflorum* var. *pansus* Blake
- Aster parvulus* Blake in Tidestr.
= *Machaeranthera parviflora* Gray
- Aster rubrotinctus* Blake in Tidestr.
Syn: *Machaeranthera rubricaulis* Rydb.; = *M. canescens* Gray
- Aster stenophyllus* D.C. Eaton, non H. & A. 1836
Syn: *A. arenarioides* D.C. Eaton; = *Erigeron arenarioides* (D.C. Eaton) Rydb.
- Aster thermalis* Jones
= *A. pauciflorus* Nutt.
- Aster venustus* Jones
= *Machaeranthera venustus* (Jones) Cronq. & Keck.
- Astragalus aboriginum* Richards.
= *A. australis* (L.) Lam.
- Astragalus amphioxys* Gray var. *cymbellus* Jones
= *A. cymboides* Jones
- Astragalus araneosus* Sheld.
= *A. lentiginosus* Dougl. var. *araneosus* (Sheld.) Barneby
- Astragalus argillosus* Jones
= *A. flavus* Nutt. var. *argillosus* (Jones) Barneby
- Astragalus argophyllus* Nutt. var. *cnicensis* Jones
= *A. argophyllus* var. *martinii* Jones
- Astragalus arietinus* Jones
= *A. cibarius* Sheld.
- Astragalus castaneiformis* var. *consobrinus* Barneby
= *A. consobrinus* (Barneby) Welsh
- Astragalus chamaeleuce* Gray in Ives var. *panguicensis* Jones
= *A. argophyllus* var. *panguicensis* (Jones) Jones
- Astragalus cicadae* var. *laccoliticus* Jones
= *A. chamaeleuce* Gray
- Astragalus coltonii* Jones var. *aphyllus* Jones
Syn: *A. coltonii* var. *coltonii*

- Astragalus confertiflorus* Gray
 = *A. flavus* var. *candicans* Gray
Astragalus decumbens (Nutt.) Gray
 = *A. miser* var. *oblongifolius* (Rydb.) Cronq. sensu Utah
Astragalus diehlii Jones
 = *A. flexuosus* var. *diehlii* (Jones) Barneby
Astragalus dodgeanus Jones
 = *A. wingatanus* Wats.
Astragalus ensiformis Jones var. *gracilior* Barneby
 = *A. ensiformis* Jones
Astragalus haydenianus Gray ex Brandegee
 = *A. bisulcatus* var. *haydenianus* (Gray) Barneby
Astragalus haydenianus Gray ex Brandegee var. *major* Jones
 = *A. bisulcatus* var. *major* (Jones) Welsh
Astragalus ibapensis Jones
 = *A. diversifolius* Gray
Astragalus junceus var. *attenuatus* Jones
 = *A. convallarius* Greene
Astragalus lentiginosus Dougl. ex Hook. var. *chartaceus* Jones
 = *A. lentiginosus* var. *araneosus* (Sheld.) Barneby
Astragalus megacarpus (Nutt.) Gray var. *caulescens* Jones
 = *A. oophorus* var. *caulescens* (Jones) Jones
Astragalus minthorniae (Rydb.) Jeps. var. *gracilior* (Barneby) Barneby
 = *A. ensiformis* Jones
Astragalus miser Dougl. ex Hook. var. *tenuifolius* (Nutt.) Barneby
 Syn: *Homalobus paucijugus* Rydb.
Astragalus newberryi Gray var. *castoreus* Jones
 = *A. newberryi* Gray
Astragalus newberryi Gray var. *wardianus* Barneby
 = *A. loanus* Barneby
Astragalus palans Jones
 = *A. lentiginosus* var. *palans* (Jones) Jones
Astragalus peabodianus Jones
 = *A. pubentissimus* var. *peabodianus* (Jones) Welsh
Astragalus pictus var. *angustus* Jones
 = *A. ceramicus* Sheld.
Astragalus pictus var. *magnus* Jones
 = *A. ceramicus* Sheld.
Astragalus preussii Gray var. *latus* Jones
 = *A. preussii* Gray var. *preussii*
Astragalus preussii Gray var. *sulcatus* Jones
 = *A. eastwoodiae* Jones
Astragalus sileranus Jones
 = *A. subcinereus* Gray
Astragalus sileranus Jones var. *caraicus* Jones
 = *A. subcinereus* Gray
Astragalus spectabilis C.L. Porter
 = *A. detritalis* Jones
Astragalus stocksii Welsh
 = *A. henrimontanensis* Welsh
Astragalus tegetarius Wats. var. *implexus* Canby ex Port. & Coult.
 = *A. kentrophyta* var. *implexus* (Canby) Barneby
Astragalus tegetarius Wats. var. *rotundus* Jones
 = *A. kentrophyta* var. *implexus* (Canby) Barneby
Astragalus thompsonae Wats.
 = *A. mollissimus* var. *thompsonae* (Wats.) Barneby
Astragalus ursinus Gray
 = *A. lentiginosus* var. *ursinus* (Gray) Barneby
Athyrium americanum (Butters) Maxon
 = *A. distentifolium* Tausch ex Opiz
Atriplex caput-medusae Eastw.
 = *A. argentea* var. *caput-medusae* (Eastw.) Fosberg
Atriplex cornuta Jones
 = *A. saccaria* Wats.
Atriplex nuttallii Wats.
 = *A. cuneata* A. Nels., inter alia
Atriplex nuttallii Wats. var. *utahensis* Jones
 = *A. tridentata* Kuntze
Atriplex patula L. var. *hastata* Gray
 = *A. triangularis* Willd.
Atriplex rydbergii Standl.
 = *A. argentea* var. *argentea*
Atriplex subdecumbens Jones
 = *A. truncata* (Torr.) Gray
Atriplex tenuissima A. Nels.
 = *A. wolfii* Wats.
Atropis laevis var. *rigida* Beal
 = *Poa canbyi* (Scribn.) Howell
Audibertiella argentea Rydb.
 = *Salvia dorrii* (Kellogg) Abrams
Aulospermum jonesii (Coult. & Rose) Coult. & Rose
 = *Cymopterus jonesii* (Coult. & Rose) Coult. & Rose
Alospermum minimum Mathias
 = *Cymopterus minimus* (Mathias) Mathias
Aulospermum rosei Jones
 = *Cymopterus rosei* (Jones) Jones
Avena mortoniana Scribn.
 = *Helicotrichon mortonianum* (Scribn.) Henrard
Azolla caroliniana authors, not Willd.
 = *A. mexicana* Presl
Bahia desertorum Jones
 = *Platyschkuhria integrifolia* var. *desertorum* (Jones) Ellison
Bahia nudicaulis Gray
 = *Platyschkuhria oblongifolia* (Gray) Rydb.
Bahia oblongifolia Gray
 = *Platyschkuhria oblongifolia* (Gray) Rydb.
Bahia ourolepis Blake
 = *Platyschkuhria oblongifolia* (Gray) Rydb.
Batidophaca humivagans Rydb.
 = *Astragalus humistratus* var. *humivagans* (Rydb.) Barneby
Batidophaca sabinarum Rydb.
 = *Astragalus argophyllus* var. *panguicensis* (Jones) Jones
Berberis fremontii Torr. in Emory
 = *Mahonia fremontii* (Torr.) Fedde
Berberis repens Lindl.
 = *Mahonia repens* (Lindl.) G. Don
Betula fontinalis Sarg.
 = *B. occidentalis* Hook.
Betula fontinalis Sarg. var. *utahensis* (Britt.) Garrett
 Syn: *B. microphylla* var. *utahensis* (Britt.) Jones; = *B. utahensis* Britt.

- Betula microphylla* var. *utahensis* (Britt.) Jones
Syn: *B. utahensis* Britt. = *B. fontinalis* var. *utahensis* (Britt.) Garrett
- Bigelovia douglasii* var. *spathulata* Jones
= *Chrysothamnus viscidiflorus* var. *pumilus* (Nutt.) Jeps.
- Bigelovia glareosa* Jones
= *C. nauseosus* (Pallas) Britt.
- Bigelovia howardii* var. *attenuata* Jones
= *Chrysothamnus parryi* var. *attenuatus* (Jones) Kittell
- Bigelovia leiosperma* var. *abbreviata* Jones
= *Chrysothamnus nauseosus* (Pallas) Britt.
- Bigelovia menziesii* var. *scopulorum* Jones
= *Haplopappus scopulorum* (Jones) Blake
- Bigelovia turbinata* Jones
= *Chrysothamnus nauseosus* var. *turbinatus* (Jones) Blake
- Blitum chenopodioides* L.
= *Chenopodium chenopodioides* (L.) Aellen
- Blitum nuttallianum* Schult. in R. & S.
= *Monolepis nuttalliana* (Schult.) Greene
- Boerhaavia torreyana* (Wats.) Standl.
= *B. spicata* Choisy
- Bouteloua hirsuta* Lag.
= Reporting error?
- Bouteloua rothrockii* Vasey
= Reporting error?
- Bouteloua uniflora* Vasey
= Reporting error?
- Brachyactis angusta* (Lindl.) Britt. in Britt. & Brown
= *Aster brachyactis* Blake. Syn: *Tripolium angustum* Lindl. in Hook.
- Brassica rapa* authors, not L.
= *B. campestris* L.
- Brickellia linifolia* D.C. Eaton
= *B. oblongifolia* Wats. var. *linifolia* (D.C. Eaton) Robins.
- Brodiaea douglasii* Wats.
= *Triteleia grandiflora* Lindl.
- Brodiaea grandiflora* (Lindl.) Macbr.
= *Triteleia grandiflora* Lindl.
- Brodiaea paysonii* A. Nels.
= *Androstephium breviflorum* Wats.
- Brodiaea pulchella* (Salisb.) Greene
= *Dichelostemma pulchellum* (Greene) Heller Syn: *Hookera pulchella* Salisb.
- Bromus catharticus* Vahl
= *B. willdenowii* Kunth
- Bromus commutatus* Schrad.
= *B. japonicus* Thunb.
- Bromus marginatus* Nees in Steud.
= *B. carinatus* H. & A.
- Bromus mollis* L.
= *B. hordeaceus* L.
- Bromus orcuttianus* Vasey
= Reporting error?
- Bromus polyanthus* Scribn. in Shear
= *B. carinatus* H. & A.
- Bromus porteri* (Coul.) Nash
= *B. anomalus* Rupr. ex Fourn.
- Bromus racemosus* L.
= *B. hordeaceus* L.
- Bromus rigidus* Roth
= *B. diandrus* Roth
- Caesalpinia repens* Eastw.
= *Hoffmanseggia repens* (Eastw.) Cockerell
- Calamagrostis inexpansa* Gray
= *C. stricta* (Timm) Koeler
- Calamagrostis montanensis* Scribn. in Vasey
= Reporting error?
- Calamagrostis neglecta* (Ehrh.) Gaertn., Mey., & Scherb.
= *C. stricta* (Timm) Koeler
- Calamagrostis rubescens* Buckl.
= Reporting error?
- Calamagrostis scopulorum* Jones var. *lucidula* Kearney
= *C. scopulorum* Jones
- Callitriche autumnalis* L.
= *C. hermaphroditica* L.
- Callitriche palustris* authors, not L.
= *C. verna* L.
- Calochortus nuttallii* T. & G. in Beckwith var. *aureus* (Wats.) Ownbey
= *C. aureus* Wats.
- Calyptridium parryi* Gray
= Reporting error?
- Calystegia sepium* (L.) R.Br.
= *Convolvulus sepium* L.
- Camassia quamash* (Pursh) Greene ssp. *utahensis* Gould
= *C. quamash* (Pursh) Greene
- Campanula petiolata* DC.
= *C. rotundifolia* L.
- Cantua aggregata* Pursh
= *Gilia aggregata* (Pursh) Spreng.
- Capnodes brachycarpum* Rydb.
= *Corydalis caseana* ssp. *brachycarpa* (Rydb.) M. Ownbey
- Cardamine cordifolia* Gray var. *pubescens* Gray ex Schulz
= *C. cordifolia* Gray
- Cardamine palustris* var. *jonesii* Kuntze
= *Rorippa curvipes* var. *curvipes*
- Cardamine uintahensis* F.J. Hermann
= *C. cordifolia* Gray
- Cardamine unijuga* Rydb.
= *C. oligosperma* Nutt.
- Carduus lacerus* Rydb.
= *Cirsium scariosum* Nutt.
- Carduus olivescens* Rydb.
= *C. scariosum* Nutt.
- Carex ablata* Bailey
= *C. luzulina* Olney
- Carex angustior* Mack. in Rydb.
= *C. muricata* L.
- Carex bolanderi* Olney
= *C. deweyana* Schwein
- Carex campylocarpa* T.H. Holm
= *C. scopulorum* T.H. Holm

- Carex campylocarpa* T. H. Holm ssp. *affinis* Maguire & Holmgren
 = *C. scopulorum* T.H. Holm
Carex canescens L. var. *dubia* Bailey
 = *C. canescens* L.
Carex chalciolepis T.H. Holm
 = *C. atrata* L.
Carex concolor Mack.
 = *C. bigelovii* Torr.
Carex drummondiana Dewey
 = *C. rupestris* All.
Carex eastwoodiana Stacey
 = *C. phaeocephala* Piper
Carex eleocharis Bailey
 = *C. stenophylla* Wahl.
Carex engelmannii Bailey
 = *C. breweri* F. Boott
Carex epapillosa Mack. in Rydb.
 = *C. atrata* L.
Carex exsiccata Bailey
 = *C. vesicaria* L.
Carex festivella Mack.
 = *C. microptera* Mack.
Carex fissuricola Mack.
 = *C. luzulina* Olney
Carex foenea authors, not Willd.?
 = *C. siccata* Dewey
Carex garberi Fern.
 = *C. aurea* Nutt.
Carex gynocrates Wormsk. ex Drejer
 = *C. dioica* L.
Carex hassei Bailey
 = *C. aurea* Nutt.
Carex hepburnii F. Boott. in Hook.
 = *C. nardina* Fries
Carex heteroneura W. Boott in Wats.
 = *C. atrata* L.
Carex interimus Maguire
 = *C. aquatilis* Wahl.
Carex kelloggii W. Boott in Wats.
 = *C. lenticularis* Michx.
Carex media R. Br. in Richards. in Franklin
 = *C. norvegica* Retz.
Carex nelsonii Mack. in Rydb.
 = *C. nova* Bailey sens. lat.
Carex pelocarpa F. Hermann
 = *C. nova* Bailey
Carex physocarpa Presl
 = *C. saxatilis* L.
Carex pityophila Mack.
 = *C. geophila* Mack.
Carex podocarpa R. Br. in Richards. var. *paysonis* (Clokey) B. Boi.
 = *C. paysonis* Clokey
Carex pseudoscirpoidea Rydb.
 = *C. scirpoidea* var. *pseudoscirpoidea* (Rydb.) Cronq.
Carex rachillis Maguire
 = *C. subnigricans* Stacey
Carex saximontana Mack.
 = *C. backii* F. Boott
Carex scirpoidea Michx. var. *curatorium* (Stacey) Cronq.
 = *C. curatorium* Stacey
Carex vernacula Bailey
 = *C. foetida* All.
Carex vernacula Bailey var. *hobsonii* Maguire
 = *C. neurophora* Mack.
Carex viridula Michx.
 = *C. oederi* Retz.
Carum garrettii A. Nels. in Coult. & Rose
 = *Perideridia gairdneri* (H. & A.) Mathias
Castilleja applegatei Fern.
 = *C. viscida* sensu Utah plants
Castilleja applegatei Fern. var. *viscida* (Rydb.) M. Ownbey
 = *C. viscida* Rydb.
Castilleja arcuata Rydb.
 = *C. linariifolia* Benth.
Castilleja minor authors, not Gray in Brewer & Wats.
 = *A. exilis* A. Nels.
Castilleja septentrionalis authors, not Lindl.
 = *C. sulphurea* Rydb.
Castilleja variabilis Rydb.
 = *C. miniata* Dougl.
Caulanthus divaricatus Rollins
 = *Thelypodopsis divaricata* (Rollins) Welsh & Reveal
Caulanthus hastatus Wats.
 = *Chlorocrambe hastatus* (Wats.) Rydb.
Ceanothus fendleri Gray var. *viridis* Jones
 = *C. fendleri* Gray
Ceanothus utahensis Eastw.
 = *C. martinii* Jones
Celtis laevigata authors, not Willd.
 = *C. reticulata* Torr.
Celtis villosula Rydb.
 = *C. reticulata* Torr.
Cenchrus pauciflorus authors, not Benth.
 = *C. longispinus* (Hack.) Fern.
Centaurium nuttallii (Wats.) Heller
 = *C. exaltatum* (Griseb.) Wight ex Piper
Cerastium variable Goodding
 = *C. beeringianum* C. & S.
Cerastium vulgatum L.
 = *C. fontanum* Baumg.
Ceratocephalus testiculatus (Crantz) Roth
 = *Ranunculus testiculatus* Crantz
Cercis orbiculata Greene
 = *C. occidentalis* var. *orbiculata* (Greene) Tidestr.
Cercocarpus flabellifolius Rydb.
 = *C. montanus* Raf.
Cercocarpus intricatus Wats. var. *villosus* Schneid.
 = *C. intricatus* Wats.
Cercocarpus ledifolius Nutt. var. *intercedens* Schneid. f. *hirsutus* Schneid.
 = *C. ledifolius* Nutt.?
Cercocarpus ledifolius Nutt. var. *intercedens* f. *subglaber* Schneid.
 = *C. ledifolius* Nutt.?

- Cercocarpus parvifolius* Woot. var. *minimus* Schneid.
= *C. montanus* Raf.?
- Chaenactis brachiata* Greene
= *C. douglasii* (Hook.) H. & A.
- Chaenactis brachiata* greene var. *stansburiana* Stockwell
= *C. douglasii* (Hook.) H. & A.
- Chamaerhodos nuttallii* (T. & G.) Pickering in Rydb.
= *C. erecta* Bunge
- Cheilanthes siliquosa* Maxon
= *Aspidotis densa* (Brackenb.) Lellinger
- Cheirinia brachycarpa* Rydb.
= *Erysimum asperum* Nutt.
- Chenopodium atrovirens* Rydb.
= *C. fremontii* Wats.
- Chenopodium berlandieri* Moq.
= *C. album* L.
- Chenopodium calceoliforme* Hook.
= *Suaeda calceoliformis* (Hook.) Moq.
- Chenopodium gigantospermum* Aellen
= *C. hybridum* L.
- Chenopodium humile* Hook.
= *C. rubrum* L.
- Chenopodium incanum* (Wats.) Heller
= *C. fremontii* Wats.?
- Chenopodium salinum* Standl.
= *C. glaucum* L.
- Chenopodium scoparium* L.
= *Kochia scoparia* (L.) Schrad.
- Chrysopsis caespitosa* Jones, not Nutt.
= *Heterotheca jonesii* (Blake) Welsh & Atwood
- Chrysopsis villosa* Nutt. var. *cinerascens* Blake
= *Heterotheca villosa* (Nutt.) Shinners
- Chrysopsis villosa* Nutt. var. *scabra* Eastw.
= *Heterotheca villosa* (Nutt.) Shinners
- Chrysothamnus marianus* Rydb.
= *C. viscidiflorus* var. *puberulus* (D.C. Eaton) Jeps.
- Chrysothamnus nauseosus* (Pallas) Britt. ssp. *albicaulis* (Nutt.) H. & C.
= *C. nauseosus* var. *albicaulis* (Nutt.) Rydb.
- Chrysothamnus nauseosus* (Pallas) Britt. ssp. *bigelovii* (Gray) H. & C.
= *C. nauseosus* var. *bigelovii* (Gray) Hall
- Chrysothamnus nauseosus* (Pallas) Britt. ssp. *consimilis* (Greene) H. & C.
= *C. nauseosus* var. *consimilis* (Greene) Hall
- Chrysothamnus nauseosus* (Pallas) Britt. ssp. *graveolens* (Nutt.) H. & C.
= *C. nauseosus* var. *graveolens* (Nutt.) Piper
- Chrysothamnus nauseosus* (Pallas) Britt. ssp. *hololeucus* (Gray) H. & C.
= *C. nauseosus* var. *gnaphaloides* (Greene) Hall sens. str.
- Chrysothamnus nauseosus* (Pallas) Britt. ssp. *junceus* (Greene) H. & C.
= *C. nauseosus* var. *junceus* (Greene) Hall
- Chrysothamnus nauseosus* (Pallas) Britt. ssp. *leiospermus* (Gray) H. & C.
= *C. nauseosus* var. *leiospermus* (Gray) Hall
- Chrysothamnus nauseosus* (Pallas) Britt. ssp. *psilocarpus* (Blake) L.C. Anderson
= *C. nauseosus* var. *psilocarpus* Blake.
- Chrysothamnus nauseosus* (Pallas) Britt. ssp. *salicifolius* (Rydb.) H. & C.
= *C. nauseosus* var. *salicifolius* (Rydb.) Hall
- Chrysothamnus nauseosus* (Pallas) Britt. ssp. *turbinatus* (Jones) H. & C.
= *C. nauseosus* var. *turbinatus* (Jones) Blake
- Chrysothamnus oliganthus* A. Nels.
= *C. nauseosus* var. *leiospermus* (Gray) Hall
- Chrysothamnus oreophilus* A. Nels.
= *C. nauseosus* var. *graveolens* (Nutt.) Piper
- Chrysothamnus parryi* (Gray) Greene ssp. *attenuatus* (Jones) H. & C.
= *C. parryi* var. *attenuatus* (Jones) Kittell
- Chrysothamnus parryi* (Gray) Greene ssp. *howardii* (Parry) H. & C.
= *C. parryi* var. *howardii* (Parry) Kittell
- Chrysothamnus parryi* (Gray) Greene ssp. *nevadensis* (Gray) H. & C.
= *C. parryi* var. *nevadensis* (Gray) Kittell
- Chrysothamnus salicifolius* Rydb.
= *C. nauseosus* (Pallas) Britt. var. *salicifolius* (Rydb.) Hall
- Chrysothamnus viscidiflorus* (Hook.) Nutt. ssp. *lanceolatus* (Nutt.) H. & C.
= *C. viscidiflorus* var. *lanceolatus* (Nutt.) Greene
- Chrysothamnus viscidiflorus* (Hook.) Nutt. ssp. *puberulus* (D.C. Eaton) H. & C.
= *C. viscidiflorus* var. *puberulus* (D.C. Eaton) Jeps.
- Chrysothamnus viscidiflorus* (Hook.) Nutt. var. *pumilus* (Nutt.) Jeps.
= *C. viscidiflorus* var. *viscidiflorus*
- Chrysothamnus viscidiflorus* (Hook.) Nutt. var. *stenophyllus* authors, not (Gray) Hall
= *C. viscidiflorus* ssp. *axillaris* (Keck) L.C. Anderson
- Chrysothamnus zionis* A. Nels.
= *C. nauseosus* var. *gnaphaloides* (Greene) Hall
- Chylismia venosa* Nels. & Kennedy
= *Camissonia multijuga* (Wats.) Raven
- Cicuta douglasii* authors, not Coult. & Rose
= *C. maculata* L.
- Circaea pacifica* Asch. & Mag.
= *Circaea alpina* L.
- Cirsium acaulescens* (Gray) K. Schum.
= *C. scariosum* Nutt.
- Cirsium drummondii* T. & G.
= *C. scariosum* Nutt.
- Cirsium eriocephalum* var. *leiocephalum* D.C. Eaton
= *C. eatonii* (Gray) Robins.
- Cirsium foliosum* authors, not (Hook.) DC.
= *C. acaulescens* (Gray) K. Schum.
- Cirsium lactucinum* Rydb.
= *C. rydbergii* Petrak
- Cirsium lanceolatum* authors, not (L.) Hill
= *C. vulgare* (Savi) Tenore
- Cirsium pulchellum* (Greene) Woot. & Standl. var. *glabrescens* Petrak
= *C. bipinnatum* (Eastw.) Petrak

- Cirsium undulatum* (Nutt.) Spreng. var. *albescens* D.C. Eaton
 = *C. undulatum* (Nutt.) Spreng.
Cladrastris lutea (Michx.) Koch
 = *C. kentukea* (Dum.-Cour.) Rudd
Claytonia chamissoi Ledeb. ex Spreng.
 = *Montia chamissoi* (Ledeb.) Robins. & Fern.
Claytonia cordifolia Wats.
 = *Montia cordifolia* (Wats.) Pax & K. Hoffm.
Claytonia lanceolata var. *rosea* (Rydb.) R.J. Davis
 = *C. lanceolata* Pursh
Claytonia perfoliata Donn
 = *Montia perfoliata* (Donn) Howell
Claytonia rosea Rydb.
 = *C. lanceolata* Pursh
Claytonia sibirica L.
 = *Montia sibirica* (L.) Howell
Claytonia triphylla Wats.
 = *Lewisia triphylla* (Wats.) Robins in Gray
Clematis alpina ssp. *occidentalis* var. *repens* Kuntze
 Syn: *C. pseudoalpina* (Kuntze) A. Nels. in Coult. & Nels.; = *C. columbiana* (Nutt.) T. & G.
Clematis columbiana authors, not (Nutt.) T. & G.
 = *C. occidentalis* (Hornem) DC.
Clematis columbiana var. *tenuiloba* (Gray) Pringle
 Syn: *C. pseudoalpina* (Kuntze) A. Nels. = *C. columbiana* (Nutt.) T. & G.
Clematis douglassii ssp. *jonesii* Kuntze
 = *C. hirsutissima* Pursh
Clematis eriophora Rydb.
 = *C. hirsutissima* Pursh
Clematis pseudoalpina (Kuntze) A. Nels. in Coult. & Nels.
 Syn: *C. alpina occidentalis repens* Kuntze = *C. columbiana* (Nutt.) T. & G.
Clematis pseudotragene ssp. *wenderothii* Kuntze
 = *C. columbiana* var. *columbiana*
Cleome integrifolia var. *angusta* Jones
 = *C. serrulata* var. *angusta* (Jones) Tidestr.
Cleomella cornuta Rydb.
 = *C. palmeriana* Jones
Cleomella nana Eastw.
 = *C. palmeriana* Jones
Clinopodium vulgare L.
 = *Satureja vulgare* (L.) Fritsch
Cnicus calcareus Jones
 = *Cirsium calcareum* (Jones) Woot. & Standl.
Cnicus clavatus Jones
 = *Cirsium clavatum* (Jones) Petrak
Cnicus nidulus Jones
 = *Cirsium nidulum* (Jones) Petrak
Cnicus rothrockii var. *diffusus* Eastw.
 = *C. rothrockii* (Gray) Petrak
Cogswellia cottamii Jones
 = *Lomatium parryi* (Wats.) Macbr.
Cogswellia millefolia var. *depauperata* Jones
 = *Lomatium grayi* Coult. & Rose
Cogswellia minima Mathias
 = *Lomatium minimum* (Mathias) Mathias
Coldenia canescens DC.
 = *Tiquilia canescens* (DC.) A. Richards.
Coldenia hispidissima (T. & G.) Gray
 = *Tiquilia latior* (Johnst.) A. Richards.
Coldenia nuttallii Hook.
 = *Tiquilia nuttallii* (Hook.) Richards.
Coleosanthus garrettii A. Nels.
 = *Brickellia grandiflora* (Hook.) Nutt.
Coloptera jonesii Coult. & Rose
 = *Cymopterus newberryi* (Wats.) Jones
Comandra linearis Rydb.
 = *C. umbellata* var. *pallida* (DC.) Jones
Cordylanthus canescens Gray
 = *C. maritimus* ssp. *canescens* (Gray) Chuang & Heckard
Cordylanthus parryi Wats. in Parry
 = *C. maritimus* ssp. *canescens* (Gray) Chuang & Heckard
Corydalis engelmannii var. *exaltata* Fedde
 = *C. aurea* Willd.
Coryphantha chlorantha Britt. & Rose
 = *C. vivipara* var. *deserti* (Engelm.) W.T. Marshall
Coryphantha marstonii Clover
 = *C. missouriensis* var. *marstonii* (Clover) L. Benson
Coryphantha vivipara (Nutt.) Britt. & Rose var. *rosea* (Clokey) L. Benson
 = Reporting error?
Cowania mexicana D. Don var. *stansburiana* (Torr.) Jeps.
 = *C. mexicana* D. Don
Cowania stansburiana Torr. in Stansb.
 = *C. mexicana* D. Don
Crassipes annuus Swallen
 = *Sclerachloa dura* (L.) Beauv.
Crataegus oxyacantha L.
 nom. ambig. = *C. monogyna* Jacq.
Crataegus rivularis Nutt. in T. & G.
 = *C. douglasii* var. *rivularis* (Nutt.) Sarg.
Crepis aculeolata Greene
 = *C. runcinata* var. *runcinata*
Crepis occidentalis Nutt. var. *costatus* Gray
 = *C. occidentalis* Nutt.
Cressa erecta Rydb.
 = *C. truxillensis* H.B.K.
Cryptantha jamesii (Torr.) Payson var. *disticha* (Eastw.) Payson
 Syn: *Oreocarya disticha* Eastw. = *O. cinerea* (Greene) Cronq. var. *cinerea*
Cryptantha jamesii (Torr.) Payson var. *multicaulis* (Torr.) Payson
 Syn: *Eritrichium multicaule* Torr.; = *O. cinerea* (Greene) Cronq.
Cryptantha jamesii (Torr.) Payson var. *pustulosa* (Rydb.) Harrington
 Syn: *Oreocarya pustulosa* Rydb. = *O. cinerea* (Greene) Cronq.
Cryptantha jamesii (Torr.) Payson var. *setosa* (Jones) Johnst. ex Tidestr.
 Syn: *Krynitzkia multicaulis* var. *setosa* Jones = *C. cinerea* (Greene) Cronq.

- Cryptantha leptophylla* Rydb.
= *C. nevadensis* Nels. & Kennedy
- Cryptantha nana* Payson var. *ovina* Payson
= *C. humilis* var. *ovina* (Payson) Higgins
- Cryptogramma acrostichoides* R. Br.
= *C. crispa* (L.) R. Br.
- Cryptogramma densa* (Brack.) Diels
= *Aspidotis densa* (Brack.) Heller
- Cuscuta californica* var. ? *squamigera* Engelm.
= *C. salina* Engelm.
- Cuscuta campestris* Yuncker
= *C. indecora* Choisy
- Cycladenia jonesii* Eastw.
= *C. humilis* var. *jonesii* (Eastw.) Welsh & Atwood
- Cymopterus calcareus* Jones
= *Cymopterus terebinthinus* (Hook.) T. & G.
- Cymopterus corrugatus* var. *coulteri* Jones
= *C. coulteri* (Jones) Mathias Syn: *Rhysopterus jonesii* Coult. & Rose
- Cymopterus corrugatus* var. *scopulicola* Jones
= *C. coulteri* (Jones) Mathias
- Cymopterus decipiens* Jones
= *C. fendleri* Gray
- Cymopterus lapidosus* var. *deserti* Jones
= *C. longipes* Wats.
- Cymopterus terebinthinus* (Hook.) T. & G. var. *calcareus* (Jones) Cronq.
Syn: *C. calcareus* Jones = *C. terebinthinus* (Hook.) T. & G.
- Cynomarathrum latilobum* Rydb.
= *Lomatium latilobum* (Rydb.) Mathias
- Cynomarathrum scabrum* Coult. & Rose
= *Lomatium scabrum* (Coult. & Rose) Math. & Const.
- Cynosurus aegypticus* L.
= *Dactyloctenium aegypticum* (L.) Beauv.
- Cynosurus indicus* L.
= *Eleusine indica* (L.) Gaertn.
- Cypripedium calceolus* L. var. *pubescens* (Willd.) Correll
= *C. calceolus* var. *parviflorum* (Schreb.) Fern.?
- Cystium stramineum* Rydb.
= *Astragalus lentiginosus* var. *stramineus* (Rydb.) Barneby
- Dalea fremontii* Torr. in Gray
= *Psorothamnus fremontii* (Torr.) Barneby
- Dalea nummularia* Jones
= *Psorothamnus polyadenius* var. *jonesii* Barneby
- Dalea polyadenia* Torr. ex Wats.
= *Psorothamnus polyadenius* (Torr.) Rydb.
- Dalea thompsonae* (Vail) L.O. Williams
= *Psorothamnus thompsonae* (Vail) Welsh & Atwood
- Datura innoxia* Mill.
= *D. fastuosa* L.
- Daucophyllum lineare* Rydb.
= *Musineon lineare* (Rydb.) Mathias
- Delphinium abietorum* Tidestr.
= *D. occidentale* Wats.
- Delphinium amabile* Tidestr.
Syn: *D. coelestinum* Rydb. = *D. scaposum* Greene
- Delphinium bicolor* Nutt.
= Reporting error?
- Delphinium coelestinum* Rydb.
Syn: *D. amabile* Tidestr. (new name) = *D. scaposum* Greene
- Delphinium leonardii* Rydb.
= *D. andersonii* Gray
- Delphinium menziesii* authors, not DC.
= *D. nuttallianum* Pritz.
- Delphinium nelsonii* Greene
= *D. nuttallianum* Pritz ex Walp.
- Delphinium scopulorum* var. *attenuatum* Jones
= *D. barbeyi* Huth.
- Descurainia pinnata* (Walt.) Britt. ssp. *paysonii* Detling
= *D. pinnata* var. *paysonii* (Detling) Welsh & Reveal
- Descurainia richardsonii* (Sweet) Schulz var. *macrosperma* Schulz
= *D. richardsonii* var. *brevipes* (Nutt.) Welsh & Reveal
- Dichanthelium lanuginosum* (Elliott) Gould
= *Panicum lanuginosum* Ell.
- Dichanthelium lanuginosum* (Elliott) Gould var. *fasciculatum* (Torr.) Spellenberg
= *Panicum lanuginosum* var. *fasciculatum* (Torr.) Fern.
- Dichanthelium oligosanthos* (Schult.) Gould
= *Panicum oligosanthos* Schult.
- Dicoria paniculata* Eastw.
= *D. canescens* Gray
- Dicoria wetherillii* Eastw.
= *D. canescens* Gray (monstrous form?)
- Dimorphocarpa wislizenii* (Engelm.) Rollins
= *Dithyrea wislizenii* Engelm.
- Dipsacus sylvestris* Huds.
= *D. fullonum* L.
- Distichlis dentata* Rydb.
= *D. stricta* (Torr.) Rydb.
- Distichlis maritima* var. *laxa* Holm
= *D. stricta* (Torr.) Rydb.
- Dodecatheon ellisiae* Standl.
= *D. dentatum* ssp. *ellisiae* (Standl.) H.J. Thompson
- Dodecatheon jeffreyi* Moore
= *D. redolens* (Hall) H.J. Thompson
- Dodecatheon meadia* var. *alpinum* Gray
= *D. alpinum* (Gray) Greene
- Dodecatheon pauciflorum* (Dur.) Greene
= *D. pulchellum* (Raf.) Merr.
- Dodecatheon radiculatum* Greene
= *D. pulchellum* (Raf.) Merr.
- Dodecatheon zionense* Eastw.
= *D. pulchellum* (Raf.) Merr.
- Draba apiculata* C.L. Hitchc.
= *D. densifolia* var. *davisiae* (C.L. Hitchc.) Welsh & Reveal
- Draba juniperina* Dorn
= *D. oligosperma* Hook.
- Draba lanceolata* authors, not Royle
= *D. cana* Rydb.
- Draba nivalis* Liljebl.
= *D. lanceolata* var. *exigua* Schulz
- Draba pectinipila* Rollins
= *D. oligosperma* var. *pectinipila* (Rollins) C.L. Hitchc.

- Draba spectabilis* Greene var. *glabrescens* Schulz
 = *D. spectabilis* Greene
Draba uncinialis Rydb.
 = *D. sobolifera* Rydb.
Draba valida Gooding
 = *D. lanceolata* Royle
Draba zionensis C.L. Hitchc.
 = *D. asprella* var. *zionensis* (C.L. Hitchc.) Welsh & Reveal
Dracocephalum nuttallii Britt. in Britt. & Brown
 = *Physostegia parviflora* Nutt.
Drymocalis micropetala Rydb.
 = *Potentilla glandulosa* ssp. *micropetala* (Rydb.) Keck
Dugaldia hoopesii (Gray) Rydb.
 = *Helenium hoopesii* Gray
Dyssodia thurberi (Gray) A. Nels.
 = *D. pentachaeta* var. *belenidum* (DC.) Strother
Echinocactus acanthodes Lem.
 = *Ferocactus acanthoides* (Lem.) Britt. & Rose
Echinocactus johnsonii Parry ex Engelm.
 = *Neolloydia johnsonii* (Parry) L. Benson
Echinocactus sileri Engelm. ex Coult.
 = *Pediocactus sileri* (Engelm.) L. Benson
Echinocactus simpsonii Engelm.
 = *Pediocactus simpsonii* (Engelm.) Britt. & Rose
Echinocactus whipplei Engelm. & Bigel.
 = *Sclerocactus parviflorus* Clover & Jotter sensu Utah
Echinocactus whipplei Engelm. & Bigel. var. *spinosior*
 Engelm. ex Boissvain
 = *Sclerocactus pubispin* (Engelm.) L. Benson
Echinocereus coccineus Engelm.
 = *E. triglochidiatus* Engelm.
Echinocereus fendleri (Engelm.) Rumpel in Forst.
 = Reporting error?
Echinopsilon hyssopifolius (Pallas) Moq. in DC.
 = *Bassia hyssopifolia* Pallas
Edwinia macrocalyx Small
 = *Jamesia americana* T. & G.
Eleocharis calva Torr.
 = *E. palustris* (L.) R. & S.
Eleocharis macrostachya Britt. in Small
 = *E. palustris* (L.) R. & S.
Elymus ambiguus Vasey & Scribn. var. *salina* (Jones)
 C.L. Hitchc.
 = *E. salina* Jones
Elymus arenicolus Scribn. & Sm. in Scribn.
 = *E. flavescens* Scribn. & Sm.
Elymus condensatus authors, not Presl
 = *E. cinereus* Scribn. & Merr.
Elymus hansenii Scribn.
 = *Elysitanion hansenii* (Scribn.) Bowden
Elymus macounii Vasey
 = *Agrohordeum macounii* (Vasey) Lepage
Emmenanthe foliosa Jones
 = *Phacelia salina* (A. Nels.) J.T. Howell
Encelia nudicaulis Gray
 = *Enceliopsis nudicaulis* (Gray) A. Nels.
Encelia nutans Eastw.
 = *Enceliopsis nutans* (Eastw.) A. Nels.
Encelia virginensis A. Nels.
 = *E. frutescens* var. *virginensis* (A. Nels.) Hall
Epilobium adenocaulon Hausskn.
 = *E. ciliatum* Raf.
Epilobium adenocaulon Hausskn. var. *occidentale* Trel.
 = *E. ciliatum* Raf.
Epilobium alpinum L.
 = *E. lactiflorum* Hausskn. in part = *E. hornemannii*
 Reichenb. in part
Epilobium brevistylum Barbey in Brewer & Wats.
 = *E. ciliatum* Raf.
Epilobium palmeri Rydb.
 = *E. saximontanum* Hausskn.
Epilobium paniculatum Nutt. ex T. & G.
 = *E. brachycarpum* Presl
Epilobium paniculatum Nutt. ex T. & G. var. *tracyi*
 (Rydb.) Munz
 Syn: *E. tracyi* Rydb. = *E. brachycarpum* Presl
Epilobium tracyi Rydb.
 Syn: *E. paniculatum* var. *tracyi* (Rydb.) Munz = *E. brachycarpum* Presl
Equisetum kansanum J.H. Schaffn.
 = *E. laevigatum* A. Br.
Equisetum prealtum Raf.
 = *E. hyemale*
Eragrostis diffusa Buckl.
 = *E. pectinacea* (Michx.) Nees
Eragrostis megastachya (Koeler) Link
 = *E. cilianensis* (All.) Mosher
Eragrostis neomexicana Vasey
 = *E. pectinacea* (Michx.) Nees
Eremocarya muricata Rydb.
 = *Cryptantha micrantha* (Torr.) Johnston.
Eremopyrum triticeum (Gaertn.) Nevski
 = *Agropyron triticeum* Gaertn.
Erigeron caespitosus Nutt. var. *laccoliticus* Jones
 = *E. caespitosus* Nutt.
Erigeron caespitosus Nutt. var. *nauseosus* Jones
 = *E. nauseosus* (Jones) Cronq.
Erigeron canadensis L.
 = *Conyza canadensis* (L.) Cronq.
Erigeron cinereus var. *aridus* Jones
 = *E. divergens* T. & G.
Erigeron concinnus (H. & A.) T. & G.
 = *E. pumilus* ssp. *concinnoideus* Cronq.
Erigeron controversus Greene
 = *E. garrettii* A. Nels.
Erigeron flagellaris Gray var. *trilobatus* Maguire & Cronq.
 = *E. proselyticus* Nesom
Erigeron fruticetorum Rydb.
 = *E. formosissimus* Greene
Erigeron gracilis Rydb.
 = *E. ursinus* D.C. Eaton
Erigeron leiophyllus Greene
 = *E. speciosus* var. *macranthus* (Nutt.) Cronq.
Erigeron macranthus Nutt.
 = *E. speciosus* var. *macranthus* (Nutt.) Cronq.

Erigeron minusculus Greene
= *E. leiomeris* Gray

Erigeron pinnatisectus A. Nels. var. *insolens* Macbr. & Payson
= *E. mancus* Rydb.

Erigeron pulvinatus Rydb. non Wedd.
= *E. compactus* Blake

Erigeron sparsifolius Eastw.
= *E. utahensis* Gray var. *sparsifolius* (Eastw.) Cronq.

Erigeron stenophyllus D.C. Eaton
= *E. arenarioides* (D.C. Eaton) Rydb.

Erigeron stenophyllus var. *tetrapleuris* Gray
= *E. utahensis* var. *tetrapleuris* (Gray) Cronq.

Eriogonum aureum Jones
= *E. corymbosum* var. *glutinosum* (Jones) Jones

Eriogonum biumbellatum Rydb.
= *E. umbellatum* var. *subaridum* Stokes

Eriogonum brevicaule Nutt. var. *pumilum* Stokes in Jones
= *E. brevicaule* var. *laxifolium* (T. & G.) Reveal

Eriogonum cernuum Nutt. var. *tenu* T. & G.
= *E. cernuum* var. *cernuum*

Eriogonum cernuum Nutt. var. *umbraticum* Eastw.
= *E. cernuum* var. *cernuum*

Eriogonum chrysocephalum Gray
= *E. brevicaule* var. *laxifolium* (T. & G.) Reveal

Eriogonum chrysocephalum Gray ssp. *alpestre* Stokes
= *E. panguicense* var. *alpestre* (Stokes) Reveal

Eriogonum confertiflorum var. *stausburyi* Benth. in DC.
= *E. brevicaule* var. *brevicaule*

Eriogonum corymbosum Benth. in DC. var. *albogilcum* Reveal
= *E. x duchesnense* Reveal

Eriogonum crispum L.O. Williams
= *E. corymbosum* var. *glutinosum* (Jones) Jones

Eriogonum deflexum Torr. in Ives ssp. *hookeri* var. *gilvum* Stokes
= *E. hookeri* Wats.

Eriogonum deflexum Torr. in Ives ssp. *ultrum* Stokes
= *E. nutans* var. *nutans*

Eriogonum dudleyanum Stokes
= *E. kearneyi* Tidestr. var. *kearneyi*

Eriogonum effusum Nutt. var. *durum* Stokes
= *E. corymbosum* var. *corymbosum*

Eriogonum effusum Nutt. ssp. *orbiculatum* Stokes
= *E. corymbosum* var. *orbiculatum* (Stokes) Reveal & Brotherson

Eriogonum effusum Nutt. ssp. *pallidum* var. *shandsii* Stokes
= *E. leptoclodon* var. *leptoclodon*

Eriogonum filicaule Stokes
= *E. subreniforme* Reveal

Eriogonum filiforme L.O. Williams
= *E. wetherillii* Eastw.

Eriogonum flexum Jones var. *ferronis* Jones
= *E. flexum* Jones

Eriogonum friscanum Jones
= *E. microthecum* var. *foliosum* (T. & G.) Reveal

Eriogonum heracleoides Nutt. var. *utahense* Gandg.
= *E. heracleoides* Nutt. var. *heracleoides*

Eriogonum kingii var. *laxifolium* T. & G.
= *E. brevicaule* Nutt. var. *laxifolium* (T. & G.) Reveal

Eriogonum longilobum Jones
= *E. shockleyi* var. *longilobum* (Jones) Reveal

Eriogonum medium Rydb.
= *E. brevicaule* Nutt. var. *laxifolium* (T. & G.) Reveal

Eriogonum nelsonii L.O. Williams
= *E. microthecum* Nutt. var. *foliosum* (Torr.) Reveal

Eriogonum nudicaule Small ssp. *garrettii* Stokes
= *E. brevicaule* Nutt. var. *brevicaule*

Eriogonum nudicaule Small ssp. *ochroflorum* Stokes
= *E. spathulatum* Gray

Eriogonum nudicaule Small ssp. *parleyense* Stokes
= *E. brevicaule* Nutt. var. *brevicaule*

Eriogonum ochrocephalum var. *angustum* Jones
= *E. brevicaule* Nutt. var. *laxifolium* (T. & G.) Reveal

Eriogonum ovalifolium Nutt. var. *utahense* Gandg.
= *E. ovalifolium* Nutt. var. *ovalifolium*

Eriogonum palmeri Wats.
= *E. plumatella* Dur. & Hilg.

Eriogonum parryi Gray
= *E. brachypodum* T. & G.

Eriogonum pauciflorum var. *panguicense* Jones
= *E. panguicense* (Jones) Reveal

Eriogonum porteri Small
= *E. umbellatum* Torr. var. *porteri* (Small) Stokes

Eriogonum pulvinatum Small
= *E. shockleyi* Wats. var. *shockleyi*

Eriogonum ramosissimum Eastw.
= *E. leptoclodon* T. & G. var. *ramosissimum* (Eastw.) Reveal

Eriogonum revealianum Welsh
= *E. corymbosum* var. *revealianum* (Welsh) Reveal

Eriogonum simpsonii Benth. in DC.
= *E. microthecum* Nutt.

Eriogonum rubiflorum Jones
= *E. nutans* T. & G. var. *nutans*

Eriogonum spathuliforme Rydb.
= *E. ostlundii* Jones

Eriogonum subalpinum Greene
= *E. umbellatum* Torr. var. *majus* Hook.

Eriogonum sulcatum Wats.
= *E. heermannii* var. *sulcatum* (Wats.) Munz & Reveal

Eriogonum sulcatum Wats. var. *argense* Jones
= *E. heermannii* Dur. & Hilg. var. *argense* (Jones) Munz

Eriogonum tenellum ssp. *cottamii* Stokes
= *E. brevicaule* var. *cottamii* (Stokes) Reveal

Eriogonum tenellum var. *grandiflorum* Gandg.
= *E. microthecum* var. *laxiflorum* Hook.

Eriogonum triste Wats.
= *E. alatum* Torr. in Sitgr.

Eriogonum umbellatum Torr. var. *glabratum* Stokes
= *E. umbellatum* Torr. var. *aureum* (Gandg.) Reveal

Eriogonum villiflorum Gray var. *tumulosum* Barneby
= *E. tumulosum* (Barneby) Reveal

Eriogonum wasatchense Jones
= *E. brevicaule* var. *wasatchense* (Jones) Reveal

- Eriophorum angustifolium* Honck.
= *E. polystachion* L.
- Eriophorum chamissonis* authors, not C.A. Mey. in Ledeb
= *E. scheuchzeri* Hoppe
- Eriophorum gracile* authors, not Koch in Roth
= *E. polystachion* L.
- Eritrichium canescens* var. *arizonicum* Gray
= *Plagiobothrys arizonicus* (Gray) Greene
- Eritrichium elongatum* Wight var. *paysonii* Johnst.
= *E. nanum* var. *elongatum* (Wight) Cronq.
- Eritrichium holopterum* Gray
= ?
- Eritrichium holopterum* Gray var. *submolle* Gray
= *Cryptantha utahensis* (Gray) Greene
- Eritrichium multicaule* Torr. in Marcy
= *Cryptantha cinerea* var. *cinerea*
- Eritrichium pterocaryum* Torr. var. *pectinatum* Gray
= *Cryptantha pterocarya* var. *pterocarya*
- Eritrichium setosissimum* Gray
= *Cryptantha setosissima* (Gray) Payson
- Erysimum capitatum* (Doug.) Greene
= *E. asperum* (Nutt.) DC.
- Erythrae calycosa* var. *arizonica* Gray
= *Centaureum calycosum* (Buckl.) Fern.
- Erythrocoma brevifolia* Greene
= *Ceum triflorum* Pursh
- Erythronium utahense* Rydb.
= *E. grandiflorum* Pursh
- Eschscholzia ludens* Greene
= *E. minutiflora* Wats.
- Espeletia amplexicaulis* Nutt.
= *Wyethia amplexicaulis* (Nutt.) Nutt.
- Eupatorium bruneri* Gray
= *E. bruneri* Gray
- Euphorbia crenulata* Engelm. in Torr.
= Reporting error?
- Euphorbia robusta* (Engelm.) Small ex Britt. & Brown var. *interioris* J.B.S. Norton
= *E. robusta* (Engelm.) Small
- Euphorbia supina* Raf.
= *E. maculata* L.
- Euploca convolvulacea* Nutt.
= *Heliotropium convolvulaceum* (Nutt.) Gray
- Eurotia lanata* (Pursh) Moq.
= *Ceratoides lanata* (Pursh) J.T. Howell
- Eurotia subspinoso* Rydb.
= *Ceratoides subspinoso* (Rydb.) J.T. Howell
- Fagus-Castanea dentata* Marsh.
= *Castanea dentata* (Marsh.) Borkh.
- Festuca brevifolia* R. Br. var. *utahensis* St-Yves
= *F. ovina* L.
- Festuca bromoides* L.
= *Vulpia bromoides* (L.) S.F. Gray
- Festuca elatior* L.
= *F. pratensis* Huds.
- Festuca fascicularis* Lam.
= *Leptochloa fascicularis* (Lam.) Gray
- Festuca grayi* (Abrams) Piper
= Reporting error?
- Festuca jonesii* Vasey
= *F. subulata* Trin.
- Festuca kingii* (Wats.) Cassidy
= *Leucopoa kingii* (Wats.) W.A. Weber
- Festuca megalura* Nutt.
= *Vulpia myuros* (L.) Gmel.
- Festuca microstachys* Nutt.
= *Vulpia microstachys* (Nutt.) Munro
- Festuca myuros* L.
= *Vulpia myuros* (L.) Gmel.
- Festuca octoflora* Walt.
= *Vulpia octoflora* (Walt.) Rydb.
- Festuca ovina* L. var. *brachyphylla* (Schult.) Piper
= *F. ovina* var. *brevifolia* (R. Br.) Wats.
- Festuca pacifica* Piper
= *Vulpia microstachys* (Nutt.) Benth.
- Festuca reflexa* Buckl.
= *Vulpia microstachys* (Nutt.) Benth.
- Fimbristylis thermalis* Wats.
= *F. spadicea* (L.) Vahl
- Floerkea occidentalis* Rydb.
= *F. proserpinacoides* Willd.
- Forestiera neomexicana* Gray
= *F. pubescens* Nutt.
- Fragaria americana* Britt.
= *F. virginiana* Duchesne
- Fragaria virginiana* Duchesne var. *glauca* Wats.
= *F. virginiana* Duchesne
- Franseria acanthicarpa* (Hook.) Cov.
= *Ambrosia acanthicarpa* Hook.
- Franseria discolor* Nutt.
= *A. tomentosa* Nutt.
- Franseria dumosa* Gray in Frem.
= *Ambrosia dumosa* (Gray) Payne
- Franseria eriocentra* Gray
= *Ambrosia eriocentra* (Gray) Payne
- Fraseria albomarginata* Wats.
= *Swertia albomarginata* (Wats.) Kuntze
- Fraseria paniculata* Torr.
Syn: *F. utahensis* Jones
- Fraseria speciosa* Dougl.
= *Swertia radiata* (Kellogg) Kuntze
- Fraseria speciosa* Dougl. var. *scabra* Jones
= *Swertia radiata* (Kellogg) Kuntze
- Fraseria utahensis* Jones
= *Swertia paniculata* (Torr.) St. John
- Fraxinus pensylvanica* Marsh. ssp. *velutina* (Torr.) G.N. Miller
= *F. velutina* Torr.
- Fritillaria dichroa* Gandg.
= *F. pudica* (Pursh) Spreng.
- Fritillaria leucella* Gandg.
= *F. pudica* (Pursh) Spreng.
- Fritillaria utahensis* Gandg.
= *F. pudica* (Pursh) Spreng.
- Funastrum heterophyllum* (Engelm.) Standl.
= *Sarcostemma cynanchoides* DCne

- Gaillardia acaulis* Gray
= *G. parryi* Greene
- Gaillardia arizonica* Gray
= Reporting error?
- Gaillardia crassifolia* Nels. & Macbr.
= *G. pinnatifida* Torr.?
- Gaillardia gracilis* A. Nels.
= *G. pinnatifida* Torr.
- Gaillardia mearnsii* Rydb.
= *G. pinnatifida* Torr.?
- Gaillardia straminea* A. Nels.
= *G. pinnatifida* Torr.
- Galium coloradoense* Wight
= *G. multiflorum* var. *coloradoense* (Wight) Cronq.
- Galium desereticum* Dempst. & Ehrend.
= *G. multiflorum* var. *multiflorum*
- Galium filipes* Rydb.
= *G. mexicanum* var. *asperulum* Gray.
- Galium hypotrichium* Gray
= *G. multiflorum* Kellogg
- Galium hypotrichium* Gray ssp. *nevadense* Dempst. & Ehrend.
= *G. multiflorum* var. *subalpinum* (Hillend. & Howell) Cronq.
- Galium hypotrichium* Gray ssp. *scabriusculum* Ehrend.
= *G. multiflorum* var. *multiflorum*
- Galium hypotrichium* ssp. *utahense* Ehrend.
= *G. multiflorum* var. *multiflorum*
- Galium magnifolium* (Dempst.) Dempst.
= *G. multiflorum* var. *multiflorum*
- Galium multiflorum* Kellogg var. *watsonii* Gray
= *G. multiflorum* var. *multiflorum* Syn: *G. watsonii* (Gray) Heller
- Galium munzii* Hilend & Howell
= *G. multiflorum* var. *multiflorum*
- Galium munzii* Hilend & Howell var. *subalpinum* Hilend & Howell
= *G. multiflorum* var. *subalpinum* (Hilend & Howell) Cronq.
- Galium scabriusculum* (Ehrend.) Dempst. & Ehrend.
= *G. multiflorum* var. *multiflorum* Syn: *G. hypotrichium* ssp. *scabriusculum* Ehrend.
- Galium scabriusculum* (Ehrend.) Dempst. & Ehrend. ssp. *protoscabriusculum* Dempst. & Ehrend.
= *G. multiflorum* var. *multiflorum*
- Galium utahense* Eastw.
= *G. boreale* L.
- Galium watsonii* (Gray) Heller
= *G. multiflorum* var. *multiflorum* Syn: *G. multiflorum* var. *watsonii* (Gray) Heller
- Gaura glandulosa* Woot. & Standl.
= Reporting error?
- Gayophytum decipiens* Lewis & Szweykowski
= *G. racemosum* T. & G.
- Gayophytum diffusum* T. & G.
= *G. ramosissimum* Nutt.
- Gayophytum diffusum* T. & G. ssp. *parviflorum* Lewis & Szweykowski
= *G. ramosissimum* Nutt.
- Gayophytum nuttallii* T. & G.
= *G. ramosissimum* Nutt.
- Gentiana barbellata* Engelm.
= *Gentianella barbellata* (Engelm.) J.M. Gillett
- Gentiana forwoodii* Gray
= *G. affinis* Griseb.
- Gentiana fremontii* Torr. ex Frem.
= *G. prostrata* Haenke
- Gentiana heterosepala* Engelm.
= *Gentianella amarella* ssp. *heterosepala* (Engelm.) Gillett
- Gentiana holopetala* (Gray) Holm
= Reporting error?
- Gentiana parryi* Engelm.
= *G. affinis* Griseb.
- Gentiana plebeia* Cham.
= *Gentianella amarella* ssp. *acuta* (Michx.) J.M. Gillett
- Gentiana romanzovii* Ledeb.
= *G. algida* Pallas
- Gentiana strictiflora* (Rydb.) A. Nels.
= *Gentianella amarella* ssp. *acuta* (Michx.) J.M. Gillett
- Gentiana tenella* Rottb. in Kiob.
= *Gentianella tenella* (Rottb.) Borner
- Gentiana tortuosa* Jones
= *Gentianella tortuosa* (Jones) Gillett
- Geranium carolinianum* L. var. *longipes* Wats.
= *G. bicknellii* Britt.
- Geum ciliatum* Pursh
= *G. triflorum* Pursh
- Gilia aggregata* (Pursh) Spreng. ssp. *aggregata* var. *attenuata* f. *utahensis* Brand
= *G. aggregata* var. *macrosiphon* Kearney & Peebles
- Gilia arenaria* Benth. var. *rubella* Brand in Engler
= *G. hutchinsifolia* Rydb.
- Gilia arizonica* (Greene) Rydb.
= *G. aggregata* var. *arizonica* (Greene) Fosberg
- Gilia breweri* Gray
= *Navarretia breweri* (Gray) Greene
- Gilia calcarea* Jones
= *G. pinnatifida* Nutt.
- Gilia clokeyi* Mason
= *G. inconspicua* var. *inconspicua*
- Gilia congesta* Hook. var. *nuda* Eastw.
= *G. roseata* Rydb. Syn: *G. nuda* (Eastw.) Rydb.
- Gilia congesta* Hook. var. *paniculata* Jones
= *G. congesta* var. *congesta*
- Gilia debilis* Wats.
= *Collomia debilis* (Wats.) Greene
- Gilia eremica* (Jeps.) Craig var. *zionis* Craig
= *Eriastrum eremicum* (Jeps.) Mason
- Gilia floribunda* var. *arida* Jones
= *Leptodactylon watsonii* (Gray) Rydb.
- Gilia frutescens* Rydb.
= *G. congesta* var. *frutescens* (Rydb.) Cronq.
- Gilia gracilis* Hook.
= *Microsteris gracilis* (Hook.) Greene
- Gilia gracilis* Hook. ssp. *spirillifera* var. *nana* Brand in Engler
= *Microsteris gracilis* (Hook.) Greene
- Gilia harknessii* Curran
= *Linanthus harknessii* (Curran) Greene

- Gilia inconspicua* (J.E. Sm.) Sweet ssp. *euinconspicua* var. *variegata* Brand in Engler
= *G. inconspicua* (J.E. Sm.) Sweet
- Gilia laxiflora* (Coul.) Osterh.
Syn: *Ipomopsis laxiflora* (Coul.) V. Grant
- Gilia leptomeria* Gray var. *tridentata* Jones
= *G. leptomeria* Gray
- Gilia mcvickerae* Jones
= *G. pinnatifida* Nutt.
- Gilia micromeria* Gray
= *G. leptomeria* var. *micromeria* (Gray) Cronq.
- Gilia ophthalmoides* Brand in Engler
= *G. inconspicua* (J.E. Sm.) Sweet
- Gilia scopulorum* Jones var. *deformis* Brand
= *G. scopulorum* Jones?
- Gilia sinuata* Dougl. ex Benth. in DC.
= *G. inconspicua* (J.E. Sm.) Sweet Syn: *G. straminea* Rydb.
- Gilia straminea* Rydb.
= *G. inconspicua* var. *sinuata* (Hook.) Gray
- Gilia superba* Eastw.
= *G. subnuda* Torr.
- Gilia tenuituba* Rydb.
= *G. aggregata* var. *macrosiphon* Kearney & Peebles
- Gilia triodon* Eastw.
= *G. leptomeria* Gray
- Gilia watsonii* Gray
= *Leptodactylon watsonii* (Gray) Rydb.
- Glandularia gooddingii* (Briq.) Solbrig
= *Verbena gooddingii* Briq.
- Glossopetalon meionandrum* Koehne
= *Forsellesia meionandra* (Koehne) Heller
- Glossopetalon nevadense* Gray
= *Forsellesia nevadensis* (Gray) Greene
- Glossopetalon spinescens* Gray
= *Forsellesia spinescens* (Gray) Greene
- Glyceria elata* (Nash) Jones
= *G. striata* (Lam.) A.S. Hitchc.
- Glyceria pauciflora* Presl
= *Puccinellia pauciflora* (Presl) Munz
- Glycosma maxima* Rydb.
= *Osmorhiza occidentalis* (Nutt.) Torr.
- Gnaphalium macounii* Greene
= *G. viscosum* H.B.K.
- Grindelia aphanactis* Rydb.
= *G. fastigiata* Greene
- Grindelia laciniata* Rydb.
= *G. fastigiata* Greene
- Grindelia stylosa* Eastw.
= *Vancelevia stylosa* (Eastw.) Greene
- Gutierrezia microcephala* (DC.) Gray
= *Xanthocephalum microcephalum* (DC.) Shinnars
- Gutierrezia sarothrae* (Pursh) Britt. & Rusby
= *Xanthocephalum sarothrae* (Pursh) Shinnars
- Gutierrezia sarothrae* (Pursh) Britt. & Rusby var. *pomariensis* Welsh
= *Xanthocephalum sarothrae* var. *pomariense* (Welsh) Welsh
- Gymnolomia hispida* Robins. & Greenm. var. *ciliata* Robins. & Greenm.
= *Helimeris hispida* (Gray) Cockerell Syn: *Viguiera ciliata* (Robins. & Greenm.) Blake
- Gymnolomia linearis* Rydb.
= *Helimeris multiflora* var. *nevadensis* (A. Nels.) Yates
- Gymnolomia multiflora* var. *annua* Jones
= *Helimeris longifolia* var. *annua* (Jones) Yates
- Hackelia jessicae* (MacGregor) Brand
= *H. micrantha* (Eastw.) Gentry
- Halostachys occidentalis* Wats.
= *Allenrolfia occidentalis* (Wats.) Kuntze
- Hamosa atratiformis* Rydb.
= *Astragalus straturensis* Jones
- Hamosa emoryana* Rydb.
= *Astragalus emoryanus* (Rydb.) Cory
- Haplopappus carthamoides* (Hook.) Gray
= Reporting error?
- Haplopappus falcatus* (Rydb.) Blake in Tidestr.
Syn: *Stenotus falcatus* Rydb. = *H. acaulis* var. *glabratus* (D.C. Eaton) Hall
- Haplopappus lyallii* Gray
= Reporting error?
- Haplopappus nelsonii* Blake in Tidestr.
Syn: *Stenotus latifolius* A. Nels. = *H. acaulis* var. *glabratus* (D.C. Eaton) Hall
- Haplopappus nuttallii* T. & G.
= *Machaeranthera grindelioides* (Nutt.) Shinnars
- Haplopappus nuttallii* T. & G. var. *depressus* Maguire
= *M. grindelioides* var. *depressa* (Maguire) Cronq. & Keck
- Haplopappus parryi* Gray
= *Solidago parryi* (Gray) Greene Syn: *H. parryi* var. *minor* Gray
- Haplopappus parryi* Gray var. *minor* Gray
= *Solidago parryi* (Gray) Greene
- Haplopappus pygmaeus* (T. & G.) Gray
= Reporting error?
- Hedeoma incana* Torr. in Emory
= *Poliomintha incana* (Torr.) Gray
- Hedeoma nana* (Torr.) Briq. in Engler & Prantl
= Reporting error?
- Hedysarum gremiale* Rollins
= *H. boreale* var. *gremiale* (Rollins) Northstrom & Welsh
- Hedysarum utahense* Rydb.
= *H. boreale* var. *boreale*
- Helianthella multicaulis* D.C. Eaton in Wats.
= *H. uniflora* (Nutt.) T. & G.
- Helianthus bracteatus* E.E. Watson
= *E. nuttallii* T. & G.
- Helianthus giganteus* var. *utahensis* D.C. Eaton in Wats.
= *H. nuttallii* T. & G.
- Heracleum lanatum* Michx.
= *H. spondylium* ssp. *montanum* (Schleich.) Briq.
- Hermidium alipes* Wats.
= *Mirabilis alipes* (Wats.) Pilz
- Hermidium alipes* Wats. var. *pallidum* C.L. Porter
= *Mirabilis alipes* (Wats.) Pilz

- Hesperanthes albomarginata* Jones
 = *Eremocrinum albomarginatum* (Jones) Jones
Hesperochloa kingii (Wats.) Rydb.
 = *Leucopoa kingii* (Wats.) W.A. Weber
Heuchera cylindrica Dougl. ex Hook.
 = Reporting error?
Heuchera utahensis Rydb.
 = *H. parvifolia* Nutt.
Heuchera versicolor Greene
 = *H. rubescens* Torr.
Heuchera versicolor Greene f. *pumila* Rosend., Butters,
 & Lakela
 = *H. rubescens* Torr.
Hieracium utahense Gandg.
 = *H. gracile* Hook.
Hippophae canadensis L.
 = *Shepherdia canadensis* L.
Holcus halepensis L.
 = *Sorghum halepense* (L.) Pers.
Holodiscus discolor (Pursh) Maxim.
 = Reporting error?
Holodiscus microphyllus Rydb.
 = *H. dumosus* (Nutt.) Heller
Homalobus canovirens Rydb.
 = *Astragalus coltonii* var. *moabensis* Jones
Homalobus humilis Rydb.
 = *Astragalus miser* var. *oblongifolius* (Rydb.) Cronq.
Homalobus paucijugus Rydb.
 = *A. miser* var. *tenuifolius* (Nutt.) Barneby Syn: *Astragalus garrettii* Macbr.
Hordeum geniculatum All.
 = *H. marinum* Huds.
Hordeum glaucum Steud.
 = *H. murinum* Huds.
Hordeum gussonianum Parl
 = *H. marinum* Huds.
Hordeum leporinum Link
 = *H. murinum* L.
Hordeum nodosum authors, not L.
 = *H. brachyantherum* Nevski
Hordeum pusillum Nutt. var. *pubens* A.S. Hitchc.
 = *H. pusillum* Nutt.
Hordeum stebbinsii Covas
 = *H. murinum* L.
Horkelia gordonii Hook.
 = *Ivesia gordonii* (Hook.) T. & G.
Horkelia mutabilis Brandege
 = *Ivesia sabulosa* (Jones) Keck
Hosackia rigida Benth. var. *nummularia* Jones
 = *Lotus longibracteatus* Rydb.
Houstonia saxicola Eastw.
 = *H. rubra* Cav.
Hymenopappus eriopodus A. Nels.
 = *H. filifolius* Hook. var. *eriopodus* (A. Nels.) Turner
Hymenopappus filifolius Hook. var. *nudipes* (Maguire)
 Turner
 Syn: *H. nudipes* Maguire = *H. filifolius* var. *alpestris*
 (Maguire) Shinners
Hymenopappus niveus Rydb.
 = *H. filifolius* var. *tomentosus* (Rydb.) Turner
Hymenopappus nudipes Maguire
 = *H. filifolius* var. *alpestris* (Maguire) Shinners
Hymenopappus nudipes Maguire var. *alpestris* Maguire
 = *H. filifolius* var. *alpestris* (Maguire) Shinners
Hymenopappus pauciflorus Johnston.
 = *H. filifolius* var. *pauciflorus* (Johnst.) Turner
Hymenopappus tomentosus Rydb.
 = *H. filifolius* var. *tomentosus* (Rydb.) Turner
Hymenoxys lemmonii (Greene) Cockerell ssp. *greenei*
 Cockerell
 = *H. lemmonii* (Greene) Cockerell
Hymenoxys richardsonii (Hook.) Cockerell var. *utahensis*
 Cockerell
 = *H. richardsonii* (Hook.) Cockerell
Hypericum perforatum L.
 = Reporting error?
Hypericum scouleri authors, not Hook.
 = *H. formosum* H.B.K.
Ilex? *myrsinites* Pursh
 = *Pachystima myrsinites* Pursh
Ipomopsis aggregata (Pursh) V. Grant ssp. *altenuata*
 (Gray) V. & A. Grant
 = *Gilia aggregata* (Pursh) Spreng.
Ipomopsis aggregata (Pursh) V. Grant ssp. *arizonica*
 (Green) V. & A. Grant
 Syn: *Callisteris arizonica* Greene = *Gilia aggregata* var.
arizonica (Greene) Fosberg
Ipomopsis aggregata (Pursh) V. Grant ssp. *formosissima*
 (Greene) Wherry
 = *Gilia aggregata* var. *maculata* Jones
Ipomopsis congesta (Hook.) V. Grant
 = *Gilia congesta* Hook.
Ipomopsis depressa (Jones) V. Grant
 = *Gilia depressa* Jones
Ipomopsis frutescens (Rydb.) V. Grant
 = *Gilia congesta* var. *frutescens* (Rydb.) Cronq.
Ipomopsis gunnisonii (T. & G.) V. Grant
 = *Gilia gunnisonii* T. & G.
Ipomopsis inconspicua J.E. Sm.
 = *Gilia inconspicua* (J.E. Sm.) Sweet
Ipomopsis laxiflora (Coult.) V. Grant
 = *Gilia laxiflora* (Coult.) Osterh.
Ipomopsis longiflora (Torr.) V. Grant
 = *Gilia longiflora* (Torr.) G. Don
Ipomopsis polycladon (Torr.) V. Grant
 = *Gilia polycladon* Torr.
Ipomopsis pumila (Nutt.) V. Grant
 = *Gilia pumila* Nutt.
Ipomopsis roseata (Rydb.) V. Grant
 = *Gilia roseata* Rydb.
Ipomopsis spicata (Nutt.) V. Grant
 = *Gilia spicata* Nutt.
Ipomopsis tenuituba (Rydb.) V. Grant
 = *Gilia aggregata* var. *macrocephala* Kearney & Peebles
Juncus albescens Fern.
 = *J. triglumis* L.
Juncus ater Rydb.
 = *J. arcticus* Willd.
Juncus balticus Willd.
 = *J. arcticus* var. *balticus* (Willd.) Trautv.

- Juncus brunnescens* Rydb.
 = *J. ensifolius* var. *brunnescens* (Rydb.) Cronq.
Juncus canadensis var. *kuntzei* Buch.
 = *J. tweedyi* Rydb.
Juncus intermedius Thuill.
 = *Luzula campestris* (L.) DC.
Juncus jonesii Rydb.
 = *J. regelii* Buch.
Juncus orthophyllus Cov.
 = Reporting error?
Juncus saximontanus A. Nels.
 = *J. ensifolius* Wikstr.
Juncus sphaerocarpus authors, not Nees ex Funk
 = *J. bufonius* L.
Juncus tracyi Rydb.
 = *J. ensifolius* Wikstr.
Juncus uncialis Greene
 = *J. kelloggii* Engelm.
Juncus utahensis Martin
 = *J. ensifolius* var. *brunnescens* (Rydb.) Cronq.
Juncus xiphoides E. Mey.
 = *J. ensifolius* Wikstr.
Juniperus californica var. *utahensis* Vasey
 = *J. osteosperma* (Torr.) Little
Juniperus californica var. *utahensis* Engelm.
 = *J. osteosperma* (Torr.) Little Syn: *J. utahensis* (Engelm.) Lemmon
Juniperus sibirica Burgsd.
 = *J. communis* var. *montana* Ait.
Juniperus utahensis (Engelm.) Lemmon
 Syn: *J. californica* var. *utahensis* Engelm.; = *J. osteosperma* (Torr.) Little
Kalmia glauca var. *microphylla* Hook.
 = *K. polifolia* var. *microphylla* (Hook.) Rehd.
Kalmia microphylla (Hook.) Heller
 = *K. polifolia* var. *microphylla* (Hook.) Rehd.
Kobresia bellardi (All.) Degland in Lois.
 Syn: *Elyna bellardii* All. = *K. sibirica* Turcz.
Kochia americana Wats. var. *vestita* Wats.
 = *K. americana* Wats.
Kochia scoparia (L.) Schrad.
 Syn: *Chenopodium scoparia* L.; = *K. iranica* Bornm.?
Koeleria cristata (L.) Pers. nom. illiget.
 = *K. macrantha* (Ledeb.) Schult.
Koeleria nitida Nutt.
 = *K. macrantha* (Ledeb.) Schult.
Krameria parvifolia Benth. var. *imparata* Macbr.
 = *K. parvifolia* Benth.
Krynitzkia echinoides Jones
 = *Cryptantha fulvocanescens* var. *echinoides* (Jones) Higgins
Krynitzkia glomerata var. *acuta* Jones
 = *Cryptantha wetherillii* (Eastw.) Payson
Krynitzkia glomerata var. *virginensis* Jones
 = *Cryptantha virginensis* (Jones) Payson
Krynitzkia leucophaea var. *alta* Jones
 = *Cryptantha confertiflora* (Greene) Payson
Krynitzkia mensana Jones
 = *Cryptantha mensana* (Jones) Payson
Krynitzkia multicaulis var. *setosa* Jones
 = *Cryptantha cinerea* (Greene) Cronq. Syn: *C. jamesii* var. *setosa* (Jones) Johnston.
Krynitzkia utahensis Gray
 = *Cryptantha utahensis* (Gray) Greene
Krynitzkia watsonii Gray
 = *Cryptantha watsonii* (Gray) Greene
Lactuca pulchella (Pursh) DC.
 = *L. tatarica* (L.) C.A. Mey.
Lactuca scariola authors, not L.
 = *L. serriola* L.
Langloisia setosissima (T. & G.) Greene var. *campyloclados* Brand
 = *L. setosissima* (T. & G.) Greene
Laphamia palmeri Gray
 = *Perityle tenella* (Jones) Macbr.
Laphamia palmeri Gray var. *tenella* Jones
 = *Perityle tenella* (Jones) Macbr.
Laphamia stansburyi Gray
 = *Perityle stansburyi* (Gray) Macbr.
Lappula collina Greene
 = *L. occidentalis* (Wats.) Greene sens. lat.
Lappula redowskii authors, not (Hornem.) Greene
 = *L. occidentalis* (Wats.) Greene
Lappula texana (Scheele) Britt.
 = *L. occidentalis* (Wats.) Greene
Larrea divaricata Cav.
 = *L. tridentata* (DC.) Cov.
Lathyrus brachycalyx Rydb. ssp. *eucosmus* (Butters & St. John) Welsh
 = *L. brachycalyx* var. *eucosmus* (Butters & St. John) Welsh
Lathyrus brachycalyx Rydb. ssp. *zionis* (C.L. Hitchc.) Welsh
 Syn: *L. zionis* C.L. Hitchc. = *L. brachycalyx* var. *zionis* (C.L. Hitchc.) Welsh
Lathyrus coriaceous White
 = *L. lanzwertii* var. *lanzwertii*
Lathyrus utahensis Jones
 = *L. pauciflorus* var. *utahensis* (Jones) Peck
Lathyrus zionis C.L. Hitchc.
 = *L. brachycalyx* var. *zionis* (C.L. Hitchc.) Welsh
Lemna minima Kunth
 = *L. minuta* H.B.K.
Lemna polyrrhiza L.
 = *Spirodela polyrrhiza* (L.) Schneid.
Lepidium brachybotryum Rydb.
 = *L. montanum* var. *montanum*
Lepidium georginum Rydb.
 = *L. lasiocarpum* var. *georginum* (Rydb.) C.L. Hitchc.
Lepidium jonesii Rydb.
 = *L. montanum* var. *jonesii* (Rydb.) C.L. Hitchc.
Lepidium montanum Nutt. in T. & G. var. *demissum* C.L. Hitchc.
 = *L. barnebyanum* Reveal
Lepidium montanum Nutt. in T. & G. var. *integrifolium* (Nutt.) C.L. Hitchc.
 = *L. integrifolium* Nutt.
Lepidium utahense Jones
 = *L. integrifolium* Nutt.

- Lepidium zionis* A. Nels.
 = *L. integrifolium* Nutt.
- Leptochloa filiformis* (L.) Beauv.
 = Reporting error?
- Leptodactylon brevifolium* Rydb.
 = *L. pungens* (Torr.) Nutt.
- Leptodactylon nuttallii* (Gray) Rydb.
 = *Linanthus nuttallii* (Gray) Ewan Syn: *Linanthus nuttallii* (Gray) Greene
- Leptotaenia eatonii* Coult. & Rose
 = *Lomatium dissectum* var. *eatonii* (Coult. & Rose) Cronq.
- Lesquerella gordonii* var. *sessilis* Wats.
 = *L. tenella* A. Nels.
- Lesquerella hitchcockii* ssp. *tumulosa* Barneby
 = *L. tumulosa* (Barneby) Reveal
- Lesquerella palmeri* Wats.
 = *L. tenella* A. Nels.
- Ligularia holmii* (Greene) W.A. Weber
 = *Senecio amplexans* var. *holmii* (Gray) Harrington
- Ligusticum brevilobum* Rydb.
 Syn: *L. porteri* var. *brevilobum* (Rydb.) Math. & Const.
 = *L. porteri* Coult. & Rose
- Ligusticum porteri* Coult. & Rose var. *brevilobum* (Rydb.) Math. & Const.
 = *L. porteri* Coult. & Rose Syn: *L. brevilobum* Rydb.
- Limnia utahensis* Rydb.
 = *Montia perfoliata* (Donn) Howell
- Limonium sinuatum* (L.) Mill
 = *Statice sinuata* L.
- Linanthus harknessii* (Curran) Greene
 Syn: *Gilia harknessii* Curran = *L. septentrionalis* Mason, sensu Utah
- Linanthus nuttallii* (Gray) Greene ex Milliken
 = *Linanthus nuttallii* (Gray) Ewan Syn: *Leptodactylon nuttallii* (Gray) Rydb.
- Linaria texana* Scheele
 = *L. canadensis* (L.) Dum.-Cours.
- Linosyris serrulata* Torr. in Stansb.
 = *Chrysothamnus viscidiflorus* var. *viscidiflorus*
- Linum aristatum* Engelm. in Wisliz. var. *subteres* Trel. in Eastwood
 = *L. subteres* (Trel.) Winkler
- Linum kingii* Wats. var. *pinetorum* Jones
 = *L. kingii* Wats.
- Linum lewisii* Pursh
 = *L. perenne* L.
- Lippia cuneifolia* (Torr.) Steud. in Marcy
 = *Phyla cuneifolia* (Torr.) Greene
- Lippia nodiflora* (L.) Michx.
 = *Phyla nodiflora* (L.) Greene
- Lippia wrightii* Gray
 = *Aloysia wrightii* (Gray) Heller
- Lithophragma bulbifera* Rydb.
 = *L. glabra* Nutt.
- Lobelia splendens* Willd.
 = *L. cardinalis* L.
- Lomatium jonesii* Coult. & Rose
 = *L. foeniculaceum* var. *macdougalii* (Coult. & Rose) Cronq.
- Lomatium macdougalii* Coult. & Rose
 = *L. foeniculaceum* var. *macdougalii* (Coult. & Rose) Cronq.
- Lomatium simplex* (Nutt.) Macbr.
 = *L. triternatum* (Pursh) Coult. & Rose
- Lophanthus urticifolius* Benth.
 = *Agastache urticifolius* (Benth.) Kuntze
- Lotus oroboides* (H.B.K.) Ottley var. *nummularius* (Jones) Isely
 = *L. longebracteatus* Rydb.
- Lupinus aegra-ovium* C.P. Sm.
 = *L. sericeus* var. *sericeus* sens. lat.
- Lupinus argentinus* Rydb.
 = *L. caudatus* Kellogg
- Lupinus argenteus* Pursh ssp. *rubricaulis* (Greene) Hess & Dunn
 = *L. argenteus* var. *rubricaulis* (Greene) Welsh
- Lupinus aridus* var. *utahensis* Wats.
 = *L. caespitosus* Nutt.
- Lupinus barbiger* Wats.
 = *L. sericeus* var. *barbiger* (Wats.) Welsh
- Lupinus eatonanus* C.P. Sm.
 = *L. leucophyllus* Dougl.
- Lupinus garrettianus* C.P. Sm.
 = *L. argenteus* var. *argenteus*
- Lupinus holosericeus* var. *utahensis* Wats.
 = *L. caudatus* var. *caudatus*
- Lupinus huffmanii* C.P. Sm.
 = *L. sericeus* var. *sericeus* sens. lat.
- Lupinus larsonanus* C.P. Sm.
 = *L. sericeus* var. *sericeus* sens. lat.
- Lupinus leucanthus* Rydb.
 = *L. jonesii* Rydb.
- Lupinus leucophyllus* Dougl. ex Lindl. var. *lupinus* Rydb.
 Syn: *L. utahensis* Moldenke = *L. caudatus* var. *caudatus*
- Lupinus marianus* Rydb.
 = *L. sericeus* var. *marianus* (Rydb.) Welsh
- Lupinus pulcher* Eastw.
 = *L. hillii* Greene
- Lupinus puroviridis* C.P. Sm.
 = *L. sericeus* var. *sericeus* sens. lat.
- Lupinus quercus-jugii* C.P. Sm.
 = *L. sericeus* var. *sericeus* sens. lat.
- Lupinus rickeri* C.P. Sm.
 = *L. sericeus* var. *sericeus* sens. lat.
- Lupinus rubens* Rydb.
 = *L. pusillus* var. *rubens* (Rydb.) Welsh
- Lupinus salinensis* C.P. Sm.
 = *L. sericeus* var. *sericeus* sens. lat.
- Lupinus sileri* Wats.
 = *L. kingii* Wats.
- Lupinus spatulatus* Rydb.
 = *L. argenteus* var. *boreus* (C.P. Sm.) Welsh
- Lupinus tenellus* Dougl. ex G. Don
 = *L. argenteus* var. *tenellus* (Dougl.) Dunn
- Lupinus tooelensis* C.P. Sm.
 = *L. prunophilus* Jones

- Lupinus watsonii* Heller
= *L. caespitosus* Nutt.
- Luzula intermedia* (Thuill.) A. Nels.
Syn: *J. intermedius* Thuill. = *L. campestris* (L.) DC.
- Luzula multiflora* (Ehrh.) Lej.
= *L. campestris* (L.) DC.
- Lychnis alba* Mill.
= *Silene alba* (Mill.) EHL Krause in Sturm
- Lychnis drummondii* (Hook.) Wats. var. *heterochroma* B. Boi.
= *L. drummondii* Wats.
- Lycium halamifolium* Mill.
= *L. barbarum* L.
- Lycopus lucidus* authors, not Turcz. ex Benth.
= *L. asper* Greene
- Lygodesmia exigua* Gray
= *Prenanthes exigua* (Gray) Rydb.
- Lygodesmia juncea* (Pursh) D. Don var. *dianthopsis* D.C. Eaton
= *L. dianthopsis* (D.C. Eaton) Tomb
- Lygodesmia spinosa* Nutt.
= *Stephanomeria spinosa* (Nutt.) Tomb
- Machaeranthera glabriuscula* (Nutt.) Cronq. & Keck var. *confertiflora* Cronq.
= *Xylorhiza confertiflora* (Cronq.) T.J. Watson
- Machaeranthera latifolia* A. Nels.
Syn: *M. rubricaulis* Rydb.; *Aster rubrotinctus* Blake = *M. bigelovii* Gray +/—
- Machaeranthera leptophylla* Rydb.
= *M. commixta* Greene?
- Machaeranthera leucanthemifolia* (Greene) Greene
Syn: *Aster leucanthemifolius* Greene
- Machaeranthera paniculata* A. Nels.
= *M. bigelovii* Gray +/—
- Machaeranthera pulverulenta* var. *vacans* A. Nels.
= *M. canescens* (Pursh) Gray?
- Machaeranthera tagetina* Greene
= Reporting error?
- Machaeranthera tortifolia* (T. & G.) Cronq. & Keck var. *imberbis* Cronq.
= *Xylorhiza tortifolia* var. *imberbis* (Cronq.) T.J. Watson
- Machaeranthera tortifolia* (T. & G.) Cronq. & Keck var. *tortifolia*
Syn: *Xylorhiza lanceolata* Rydb. = *Xylorhiza tortifolia* (T. & G.) Greene
- Machaeranthera venusta* (Jones) Cronq. & Keck
Syn: *Aster venusta* Jones = *Xylorhiza venusta* (Jones) Heller
- Macronema obovatum* Rydb.
= *Haplopappus rydbergii* Blake
- Madronella oblongifolia* Rydb.
= *Monardella odoratissima* Benth.
- Madronella parvifolia* Greene
= *Monardella odoratissima* Benth.
- Madronella sessilifolia* Rydb.
= *Monardella odoratissima* Benth.
- Malvastrum exile* Gray in Ives
= *Eremalche exilis* (Gray) Greene
- Mammillaria chlorantha* Engelm. in Wheeler
= *Coryphantha vivipara* var. *deserti* (Engelm.) W.T. Marshall
- Mammillaria vivipara* (Nutt.) Haw.
= *Coryphantha vivipara* (Nutt.) Britt. & Rose
- Marsilea mucronata* A. Br.
= *M. vestita* Hook. & Grev.
- Matricaria inodora* L.
= *M. maritima* L.
- Matricaria matricarioides* (Less.) T.C. Porter
= *Chamomilla suaveolens* (Pursh) Rydb.
- Matricaria parthenium* L.
= *Chrysanthemum parthenium* (L.) Bernh.
- Mentha borealis* Michx.
= *M. arvensis* L.
- Mentha canadensis* L.
= *M. arvensis* L.
- Mentzelia albicaulis* Dougl. in Hook. var. *integrifolia* Wats.
= *M. dispersa* Wats.
- Mentzelia montana* (A. Davids.) A. Davids.
= Reporting error?
- Mentzelia multiflora* (Nutt.) Gray var. *integra* Jones
= *M. integra* (Jones) Tidestr.
- Mentzelia rusbyi* Woot.
= *M. nuda* (Pursh) T. & G.
- Mertensia bakeri* Greene
= *M. viridis* A. Nels.
- Mertensia leonardii* Rydb.
= *M. arizonica* Greene var. *leonardii* (Rydb.) Johnst.
- Mertensia paniculata* var. *nivalis* Wats.
= *M. viridis* A. Nels. var. *cana* (Rydb.) L.O. Williams
- Mertensia praecox* Smiley in Macbr.
= *M. oblongifolia* var. *nevadensis* (A. Nels.) L.O. Williams
- Mertensia sampsonii* Tidestr.
= *M. arizonica* var. *leonardii* (Rydb.) Johnst.
- Mertensia toyabensis* var. *subnuda* Macbr.
= *M. arizonica* var. *subnuda* (Macbr.) L.O. Williams
- Micropuntia barkleyana* Daston
= *Opuntia pulchella* Engelm.
- Micropuntia brachyrophalica* Daston
= *Opuntia pulchella* Engelm.
- Micropuntia spectatissima* Daston
= *Opuntia pulchella* Engelm.
- Microsteris humilis* Greene
= *M. gracilis* (Hook.) Greene
- Mimulus glabratus* H.B.K. ssp. *utahensis* Pennell
= *M. glabratus* H.B.K.
- Mimulus pilosus* (Benth.) Wats.
= *Mimetanthe pilosa* (Benth.) Greene
- Minuartia austromontana* S.J. Wolf & Packer
= *Arenaria rossii* Richards.
- Mirabilis glutinosa* A. Nels.
= *M. bigelovii* Gray var. *retrorsa* (Heller) Munz
- Mirabilis linearis* (Pursh) Heimerl.
= *Oxybaphus linearis* (Pursh) Robins.
- Mitella stenopetala* Piper
= *M. stauropetala* Piper

Moldavica parviflora (Nutt.) Britt. in Britt. & Br.
= *Dracocephalum parviflorum* Nutt.

Moldavica thymifolia (L.) Rydb.
= *Dracocephalum thymifolium* L.

Monarda menthaefolia Graham
= *M. fistulosa* var. *menthaefolia* (Graham) Fern.

Monardella glauca Greene
= *M. odoratissima* var. *glauca* (Greene) St. John

Mortonia scabrella Gray var. *utahensis* Cov. in Gray
= *M. scabrella* Gray

Mortonia utahensis (Cov.) A. Nels.
= *M. scabrella* Gray

Muhlenbergia curtifolia Scribn.
= *M. thurberi* Rydb.

Muhlenbergia minutissima (Steud.) Swallen
= Reporting error?

Muhlenbergia polycaulis Scribn.
= Reporting error?

Muhlenbergia repens (Presl) A.S. Hitchc. in Jeps.
= Reporting error?

Myosurus apetalus authors, not C. Gay
= *M. aristatus* Benth.

Myosurus nitidus Eastw.
= Reporting error?

Myriophyllum verticillatum L.
= *M. spicatum* L.

Najas flexilis ssp. *caespitosus* Maguire
= *N. caespitosus* (Maguire) Reveal

Navaretia minima authors, not Nutt.
= *N. intertexta* (Benth.) Hook.

Navaretia propinqua Suksd.
= *N. intertexta* (Benth.) Hook.

Navaretia setosissima T. & G. in Ives
= *Langloisia setosissima* (T. & G.) Greene

Nolina bigelovii (Torr.) Wats.
= *N. microcarpa* Wats., sensu Utah

Nuttallia lobata Rydb.
= *Mentzelia integra* (Jones) Tidestr.

Oenothera albicaulis Pursh var. *decumbens* Wats. ex Parry
= *O. deltoidea* ssp. *ambigua* (Wats.) W. Klein

Oenothera alyssoides H. & A.
= *Camissonia boothii* ssp. *alyssoides* (H. & A.) Raven

Oenothera alyssoides H. & A. var. *minutiflora* Wats.
= *Camissonia minor* (A. Nels.) Raven

Oenothera alyssoides Pursh var. *villosa* Wats.
= *Camissonia boothii* ssp. *alyssoides* (H. & A.) Raven

Oenothera ambigua Wats.
= *O. deltoidea* var. *ambigua* (Wats.) Munz

Oenothera andina Nutt. in T. & G.
= *Camissonia andina* (Nutt.) Raven

Oenothera boothii Dougl. ex Hook.
= *Camissonia boothii* (Dougl.) Raven

Oenothera breviflora T. & G.
= *Camissonia breviflora* (T. & G.) Raven

Oenothera brevipes var. *pallidula* Munz
= *Camissonia brevipes* var. *pallidula* (Munz) Raven

Oenothera brevipes var. *parviflora* Wats. in Parry
= *Camissonia multijuga* (Wats.) Raven

Oenothera caespitosa Nutt. ssp. *jonesii* (Munz) Munz
= *O. caespitosa* var. *jonesii* Munz

Oenothera californica ssp. *avita* W. Klein
= *O. avita* (W. Klein) W. Klein

Oenothera chamaenerioides Gray
= *Camissonia chamaenerioides* (Gray) Raven

Oenothera clavaeformis Torr. & Frem.
= *Camissonia clavaeformis* (Torr. & Frem.) Raven

Oenothera contorta Dougl. ex Hook.
= *Camissonia contorta* (Dougl.) Raven

Oenothera decorticans Greene var. *condensata* Munz
= *Camissonia boothii* ssp. *condensata* (Munz) Raven

Oenothera eastwoodiae (Munz) Raven
= *Camissonia eastwoodiae* (Munz) Raven

Oenothera gauraeflora var. *hitchcockii* H. Lev.
= *Camissonia boothii* ssp. *alyssoides* (H. & A.) Raven

Oenothera glabella Nutt. in T. & G.
= *Boisduvalia glabella* (Nutt.) Walpers

Oenothera heterantha Nutt.
= *Camissonia subacaulis* (Pursh) Raven

Oenothera latifolia (Rydb.) Munz
= *O. pallida* Lindl. sens. lat.

Oenothera lavandulaefolia T. & G.
= *Calylophus lavandulaefolia* (T. & G.) Raven

Oenothera megalantha (Munz) Raven
= *Camissonia megalantha* (Munz) Raven

Oenothera minor (A. Nels.) Munz
= *Camissonia minor* (A. Nels.) Raven

Oenothera multijuga Wats.
= *Camissonia multijuga* (Wats.) Raven

Oenothera multijuga Wats. var. *orientalis* Munz
= *Camissonia walkeri* ssp. *walkeri*

Oenothera pallidula (Munz) Munz
= *Camissonia brevipes* ssp. *pallidula* (Munz) Raven

Oenothera parryi Wats. ex Parry
= *Camissonia parryi* (Wats.) Raven

Oenothera pterosperma Wats.
= *Camissonia pterosperma* (Wats.) Raven

Oenothera refracta Wats.
= *Camissonia refracta* (Wats.) Raven

Oenothera runcinata (Engelm.) Munz
= *O. pallida* ssp. *runcinata* (Engelm.) Munz & Klein

Oenothera rydbergii House
= *O. villosa* Thunb.

Oenothera scapoidea Nutt. in T. & G.
= *Camissonia scapoidea* (Nutt.) Raven

Oenothera scapoidea Nutt. in T. & G. ssp. *utahensis* Raven
= *Camissonia scapoidea* ssp. *utahensis* (Raven) Raven

Oenothera strigosa (Rydb.) Mack. & Bush
Syn: *O. rydbergii* House = *O. villosa* Thunb.

Oenothera subacaulis (Pursh) Garrett
= *Camissonia subacaulis* (Pursh) Raven

Oenothera tenuissima Jones
= *Camissonia parryi* (Wats.) Raven

Oenothera trichocalyx Nutt. in T. & G.
= *O. pallida* ssp. *trichocalyx* (Nutt.) Munz & Klein

- Oenothera triloba* var. *ecristata* Jones
= *O. flava* (A. Nels.) Garrett
- Oenothera walkeri* (A. Nels.) Raven
= *Camissonia walkeri* (A. Nels.) Raven
- Opuntia aurea* Baxter
= *O. basilaris* var. *aurea* (Baxter) W.T. Marshall
- Opuntia barbata* K. Brand. ex J.A. Purpus
= *O. polyacantha* (?)Haw.
- Opuntia barbata* K. Brandeggee ex J.A. Purpus var. *gracilima* K. Brandeggee ex J.A. Purpus
= *O. polyacantha* (?)Haw.
- Opuntia compressa* Macbr.
= *O. macrorhiza* Engelm. sens. lat.
- Opuntia erinacea* Engelm. var. *xanthostema* (K. Schum.) L. Benson
= *O. erinacea* var. *utahensis* (Engelm.) L. Benson
- Opuntia fragilis* (Nutt.) Haw. var. *denudata* Weigand & Backebg.
= *O. fragilis* var. *fragilis*?
- Opuntia palmeri* Engelm.
= ? *O. phaeacantha* var. *discata* (Griffiths) Benson & Walkington
- Opuntia rhodantha* K. Schumann
= *O. polyacantha* var. *utahensis* (Engelm.) L. Benson
- Opuntia rubrifolia* Engelm.
= *O. erinacea* var. *ursina* Parish
- Opuntia sphaerocarpa* var. *utahensis* Engelm.
= *O. erinacea* var. *utahensis* (Engelm.) L. Benson
- Opuntia utahensis* J.A. Purpus
= *O. macrorhiza* Engelm.
- Oreocarya breviflora* Osterh. in Payson
= *Cryptantha breviflora* (Osterh.) Payson
- Oreocarya commixta* Macbr.
= *Cryptantha humilis* var. *commixta* (Macbr.) Higgins
- Oreocarya disticha* Eastw.
Syn: *Cryptantha jamesii* var. *disticha* (Eastw.) Payson = *C. cinerea* (Greene) Cronq.
- Oreocarya dolosa* Macbr.
= *Cryptantha humilis* var. *shantzii* (Tidestr.) Higgins
- Oreocarya jonesiana* Payson
= *Cryptantha jonesiana* (Payson) Payson
- Oreocarya nana* Eastw.
= *Cryptantha humilis* var. *nana* (Eastw.) Higgins
- Oreocarya pustulosa* Rydb.
= *Cryptantha pustulosa* (Rydb.) Payson Syn: *C. jamesii* var. *pustulosa* (Rydb.) Harrington
- Oreocarya rugulosa* Payson
= *Cryptantha rugulosa* (Payson) Payson
- Oreocarya shantzii* Tidestr.
= *Cryptantha humilis* var. *shantzii* (Tidestr.) Higgins
- Oreocarya tenuis* Eastw.
= *Cryptantha tenuis* (Eastw.) Payson
- Oreocarya tora* A. Nels.
= *Cryptantha flava* (A. Nels.) Payson
- Oreocarya wetherillii* Eastw.
= *Cryptantha wetherillii* (Eastw.) Payson
- Oreocarya williamsii* A. Nels.
= *Cryptantha stricta* (Osterh.) Payson
- Orbanche californica* C. & S.
= Reporting error
- Oryzopsis bloomeri* (Boland.) Ricker
= *Stiporyzopsis bloomeri* (Boland.) B.L. Johnson
- Osmorhiza obtusa* (Coul. & Rose) Fern.
= *O. depauperata* Phil.
- Osmunda crispa* L.
= *Cryptogramma crispa* (L.) R.Br.
- Oxybaphus angustifolia* var. *viscidus* Eastw.
= *O. linearis* (Pursh) Robins.
- Oxytropis obnapiformis* C.L. Porter
= *O. besseyi* var. *obnapiformis* (C.L. Porter) Welsh
- Pachylophus crinitus* Rydb.
= *Oenothera caespitosa* var. *crinita* (Rydb.) Munz
- Panicum crus-galli* L.
= *Echinochloa crus-galli* (L.) Beauv.
- Panicum dactylon* L.
= *Cynodon dactylon* (L.) Pers.
- Panicum hallii* Vasey
= Reporting error?
- Panicum huachucae* Ashe
Syn: *Dichanthelium lanuginosum* var. *fasciculatum* (Torr.) Spellenberg; = *Panicum lanuginosum* Ell. var. *fasciculatum* (Torr.) Fern.
- Panicum scribnerianum* Nash
Syn: *Dichanthelium oligosanthos* (Schult.) Gould.; = *Panicum oligosanthos* Schult.
- Panicum tennesseense* Ashe
= *P. lanuginosum* var. *fasciculatum* (Torr.) Fern.
- Panicum thermale* Boland.
= *P. lanuginosum* (Ell.) Gould. sens. lat.
- Panicum verticillatum* L.
= *Setaria verticillata* (L.) Beauv.
- Panicum viride* L.
= *Setaria viridis* (L.) Beauv.
- Papaver kluanense* Love
= *P. radicatum* Rottb. in DC.
- Pappophorum wrightii* Wats.
= *Enneapogon desvauxii* Beauv.
- Parietaria obtusa* Rydb. in Small
= *P. floridana* Nutt.
- Parassia parviflora* DC.
= *P. palustris* L.
- Parosela thompsonae* Vail
= *Psoralea thompsoniae* (Vail) Welsh & Atwood
- Parrya platycarpa* Rydb.
= *P. rydbergii* Botsch.
- Parthenium alpinum* (Nutt.) T. & G. var. *ligulatum* Jones
Syn: *Bolophytia ligulata* (Jones) W.A. Weber = *P. ligulatum* (Jones) Barneby
- Parthenocissus vitacea* (Knerr) A.S. Hitchc.
= *P. inserta* (Kerner) K. Fritsch
- Pedicularis crenulata* Benth. in DC.
- Pedicularis paysoniana* Pennell
= *P. bracteosa* var. *paysoniana* (Pennell.) Cronq.
- Pediocactus hermannii* W.T. Marshall
= *P. simpsonii* (Engelm.) Britt. & Rose
- Pellaea jonesii* (Maxon) Morton
= *Notholaena jonesii* Maxon
- Pellaea limitanea* (Maxon) Morton
= *Notholaena limitanea* Maxon

Pellaea longimucronata Hook.

= *P. truncata* Goodding

Pellaea suksdorfiana Butters

= *P. glabella* Mett.

Penstemon acuminatus Dougl. var. *congestus* Jones

Syn: *P. pachyphyllus* ssp. *congestus* (Jones) Keck; do var.

congestus (Jones) N. Holmgr. = *P. congestus* (Jones)

Pennell

Penstemon angustifolius Nutt. ssp. *venosus* Keck in Kearney & Peebles

= *P. angustifolius* var. *venosus* (Keck) N. Holmgren

Penstemon azureus var. *ambiguus* Gray

= *P. sepallulus* A. Nels.

Penstemon caespitosus Nutt. ex Gray var. *suffruticosus* Gray

= *P. tusharensis* N. Holmgren

Penstemon cleburnei Jones

= *P. eriantherus* Pursh

Penstemon confertus var. *aberrans* Jones

= *P. procerus* var. *aberrans* (Jones) A. Nels.

Penstemon crandallii A. Nels. ssp. *atratus* Keck

= *P. crandallii* var. *atratus* (Keck) N. Holmgren

Penstemon cyananthus Hook. ssp. *compactus* Keck

= *P. compactus* (Keck) Crosswhite

Penstemon cyananthus Hook. ssp. *longiflorus* Pennell

= *P. longiflorus* (Pennell) S. Clark

Penstemon eatonii Gray ssp. *undosus* (Jones) Keck

= *P. eatonii* var. *undosus* Jones

Penstemon garrettii Pennell

= *P. scariosus* Pennell sens. lat.

Penstemon glaber var. *utahensis* Wats.

= *P. subglaber* Rydb.

Penstemon heterophyllus var. *latifolius* Wats.

= *P. platyphyllus* Rydb.

Penstemon jamesii Benth. in DC. ssp. *ophianthus* (Pennell) Keck

= *P. ophianthus* Pennell

Penstemon kingii Wats.

= Reporting error?

Penstemon obtusifolius Pennell

= *P. humilis* var. *obtusifolius* (Pennell) Reveal

Penstemon osterhoutii authors, not Pennell

= *P. mucronatus* N. Holmgren

Penstemon palmeri Gray ssp. *eglandulosus* Keck

= *P. palmeri* var. *eglandulosus* (Keck) N. Holmgren

Penstemon phlogifolius Green

= *P. watsonii* Gray

Penstemon pseudohumilis Jones

= *P. marcusii* (Keck) N. Holmgren?

Penstemon pumilus var. *thompsoniae* Gray

Syn: *P. caespitosus* var. *thompsoniae* (Gray) A. Nels. =

P. thompsoniae (Gray) Rydb.

Penstemon venosus (Keck) Reveal

= *P. angustifolius* var. *venosus* (Keck) N. Holmgren

Petalostemon flavescens Wats.

= *Dalea flavescens* (Wats.) Welsh

Petalostemon occidentale (Heller) Fern.

= *Dalea oligophylla* (Torr.) Shinners

Petalostemon searlsiae Gray

= *Dalea searlsiae* (Gray) Barneby

Peucedanum bicolor Wats.

= *Lomatium bicolor* (Wats.) Coult. & Rose

Peucedanum graveolens Wats.

= *Lomatium nuttallii* (Gray) Macbr.

Peucedanum juniperinum Jones

= *Lomatium juniperinum* (Jones) Coult. & Rose

Peucedanum lapidosum Jones

= *Cymopterus longipes* Wats.

Peucedanum parryi Wats.

= *Lomatium parryi* (Wats.) Macbr.

Peucedanum triternatum var. *platycarpum* Torr. in Standb.

= *Lomatium triternatum* var. *platycarpum* (Torr.) Cronq.

Phaca mollissima var. *utahensis* Torr. & Stansb.

= *Astragalus utahensis* (Torr.) T. & G.

Phaca pardalina Rydb.

= *Astragalus pardalinus* (Rydb.) Barneby

Phaca salsula Pallas

= *Sphaerophysa salsula* (Pallas) DC.

Phacelia foetida Goodding

= *P. palmeri* Torr.

Phacelia leucophylla Torr. in Frem.

= *P. hastata* Dougl. ex Lehm.

Phacelia nudicaulis Eastw.

= *P. demissa* Gray var. *demissa*

Phacelia orbicularis Rydb.

= *P. corrugata* A. Nels.

Phacelia pinetorum Jones

= *Eucrypta micrantha* Torr.

Phacelia pulchella Gray var. *sabulonum* J.T. Howell

= *P. pulchella* Gray

Phalangium quamash Pursh

= *Camassia quamash* (Pursh) Greene

Phalaris oryzoides L.

= *Leersia oryzoides* (L.) Swartz

Phalaris semiverticillata Forsk.

= *Polypogon semiverticillata* (Forsk.) Hylander

Philadelphus nitidus A. Nels.

= *P. microphyllus* Gray

Phlox bryoides Nutt.

= *P. muscoides* Nutt.

Phlox caesia Eastw.

= *P. gladiformis* (Jones) E. Nels.

Phlox caespitosa authors, not Nutt.

= *P. pulvinata* (Wherry) Cronq.

Phlox caespitosa ssp. *pulvinata* Wherry

= *P. pulvinata* (Wherry) Cronq.

Phlox canescens T. & G. in Beckwith

= *P. hoodii* var. *canescens* (T. & G.) Peck

Phlox densa Brand.

= *P. austromontana* Cov.

Phlox grahamii Wherry

= *P. longifolia* Nutt.

Phlox hoodii Richards. var. *canescens* (T. & G.) Peck

= *P. hoodii* Richards.

Phlox jonesii Wherry

= *P. austromontana* var. *prostrata* E. Nels.

Phlox longifolia Nutt. var. *glandiformis* Jones

= *P. gladiformis* (Jones) E. Nels.

Phlox speciosa var. *stansburyi* Torr. in Emory

= *P. longifolia* var. *stansburyi* (Torr.) Gray

Phlox stansburyi (Torr.) Heller

= *P. longifolia* var. *stansburyi* (Torr.) Gray

Phragmites communis Trin.

= *P. australis* (Cav.) Trin.

Physalis fendleri Gray var. *cordifolia* Gray

= *P. hederacfolia* var. *cordifolia* (Gray) Waterfall

Physalis longifolia Nutt.

= *P. virginiana* Mill.

Physaria australis (Payson) Rollins

= *P. acutifolia* Rydb.

Pinus contorta Dougl. ex Loud. var. *latifolia* Engelm. ex Wats.

= *P. contorta* Dougl.

Plantago major L. var. *pachyphylla* Pilger

= *P. major* L.

Plantago purshii R. & S.

= *P. patagonica* Jacq.

Platystemon remotus Greene

= *P. californicus* Benth.

Platystemon rigidulus Greene

= *P. californicus* Benth.

Platystemon terminii Fedde

= *P. californicus* Benth.

Pleurophragma platypodium Rydb.

= *Thelypodium integrifolium* var. *gracilipes* Robins.

Poa airoides Nutt.

= *Puccinellia airoides* (Nutt.) Wats. & Coult.; *P. nuttalliana* (Schult.) A.S. Hitchc.

Poa ampla Merr.

= *P. secunda* Presl

Poa canbyi (Scribn.) Howell

Syn: *Atropis laevis* var. *rigida* Beal; = *P. secunda* Presl

Poa curta Rydb.

= *P. nervosa* (Hook.) Vasey

Poa cusickii Vasey

= *P. fendleriana* (Steud.) Vasey sens. lat.

Poa distans L.

= *Puccinellia distans* (L.) Parl

Poa eatonii Wats.

= *P. fendleriana* (Steud.) Vasey

Poa epilis Scribn.

= *P. fendleriana* (Steud.) Vasey sens. lat.

Poa fasciculata Torr.

= *Puccinellia fasciculata* (Torr.) Bicknell

Poa festucoides Jones

= *Festuca thurberi* Vasey

Poa gracillima Vasey

= *P. secunda* Presl

Poa interior Rydb.

= *P. glauca* Vahl

Poa juncifolia Scribn.

= *P. secunda* Presl

Poa kingii Wats.

= *Leucopha kingii* (Wats.) W.A. Weber

Poa longiligula Scribn. & Will.

= *P. fendleriana* (Steud.) Vasey sens. lat.

Poa nevadensis Vasey ex Scribn.

= *P. secunda* Presl

Poa nuttalliana Schult. in R. & S.

= *Puccinellia nuttalliana* (Schult.) A.S. Hitchc.

Poa reflexa Vasey & Scribn.

= *P. leptocoma* Trin.

Poa rupicola Nash in Rydb.

= *P. glauca* Vahl

Poa sandbergii Vasey

= *P. secunda* Presl

Poa scabrella (Thurb.) Benth. ex Vasey

= *P. secunda* Presl

Poa scabriuscula Williams

= *P. fendleriana* (Steud.) Vasey

Poa wolfii Scribn.

= Reporting error?

Polanisia trachysperma T. & G.

= *P. dodecandra* var. *trachysperma* (T. & G.) Iltis

Polemonium albidiflorum Eastw.

= *P. foliosissimum* var. *alpinum* Brand.

Polemonium caeruleum L.

= *P. occidentale* Greene sens. str.

Polemonium delicatum Rydb.

= *P. pulcherrimum* var. *delicatum* (Rydb.) Cronq.

Polemonium foliosissimum Gray ssp. *albidiflorum* (Eastw.) Brand

= *P. foliosissimum* ssp. *albiflorum* var. *alpinum* Brand

Polygala acanthoclada Gray var. *intricata* Eastw.

= *P. acanthoclada* Gray

Polygonum coccineum Muhl ex Willd.

= *P. amphibium* L.

Polygonum engelmannii Greene

= *P. douglasii* Greene

Polygonum watsonii Small

= *P. kelloggii* Greene

Polypodium bulbiferum L.

= *Cystopteris bulbifera* (L.) Bernh.

Polypodium felix-mas L.

= *Dryopteris felix-mas* (L.) Schott.

Polypodium fragile L.

= *Cystopteris fragilis* (L.) Bernh.

Polypodium lonchitis L.

= *Polystichum lonchitis* (L.) Roth

Polypogon lutosus authors, not (Poir.) A.S. Hitchc.

= *P. interruptus* H.B.K.

Populus aurea Tidestr.

= *P. tremuloides* Michx.

Populus tremuloides Michx. var. *aurea* (Tidestr.) Sarg.

Syn: *P. aurea* Tidestr.; = *P. tremuloides* Michx.

Potamogeton diversifolius Raf.

= Reporting error?

Potamogeton latifolius (Robbins) Morong

= *P. filiformis* var. *latifolius* (J.W. Robins) Reveal

Potamogeton perfoliatus L. var. *richardsonii* Bennett

= *P. richardsonii* (Bennett) Rydb.

Potamogeton pusillus L. var. *vulgaris* subvar. *interruptus* J.W. Robbins
= *P. pusillus* var. *pusillus*

Potamogeton zosteriformis Fern.
= Reporting error?

Potentilla bicrenata Rydb.
= *P. concinna* var. *bicrenata* Welsh & Johnston

Potentilla decurrens (Wats.) Rydb.
Syn: *P. diversifolia* var. *decurrens* (Wats.); *P. plattensis* authors, not Nutt.; = *P. ovina* var. *decurrens* (Wats.) Welsh & Johnston.

Potentilla dissecta var. *decurrens* Wats.
Syn: *P. decurrens* (Wats.) Rydb. = *P. ovina* var. *decurrens* (Wats.) Welsh & Johnston

Potentilla diversifolia Lehm. var. *decurrens* (Wats.) Th. W.
= *P. ovina* var. *decurrens* (Wats.) Welsh & Johnston

Potentilla diversifolia var. *pinnatisecta* Wats.
= *P. ovina* Macoun

Potentilla gracilis Dougl. var. *pulcherrima* (Lehm.) Fern.
= *P. pulcherrima* Lehm.

Potentilla modesta Rydb.
= *P. concinna* var. *modesta* (Rydb.) Welsh & Johnston

Potentilla ovina Macoun. var. *decurrens* (Wats.) Welsh & Johnston

Syn: *P. dissecta* var. *decurrens* Wats.

Potentilla paucijuga Rydb.
= *P. pensylvanica* var. *paucijuga* (Rydb.) Welsh & Johnston

Potentilla proxima Rydb.
= *P. concinna* var. *proxima* (Rydb.) Welsh & Johnston

Potentilla sabulosa Jones
= *Ivesia sabulosa* (Jones) Keck

Potentilla wardii Greene
= *P. hippiana* Lehm.

Potentilla wheeleri Wats.
= Reporting error?

Proboscidea louisianica not (Mill.) Thell.
= *P. parviflora* (Woot.) Woot. & Standl. sensu Utah

Prosartes trachycarpa Wats.
= *Disporum trachycarpum* Wats.

Prunella pensylvanica var. *lanceolata* Barton.
= *P. vulgaris* L. var. *lanceolata* (Barton) Fern.

Prunus amygdalus Batsch.
= *P. dulcis* (Miller) D.A. Webb.

Prunus cerasus var. *avium* L.
= *P. avium* (L.) L.

Psathyrotes ramosissima (Torr.) Gray
= Reporting error?

Pseudocymopterus montanus (Gray) Coult. & Rose
= *Cymopterus lemmonii* (Coult. & Rose) Dorn

Pseudocymopterus tidesstromii Coult. & Rose
= *Cymopterus lemmonii* (Coult. & Rose) Dorn

Pseudocymopterus versicolor Rydb.
= *Cymopterus lemmonii* (Coult. & Rose) Dorn

Pseudopteryxia longiloba Rydb.
= *Cymopterus hendersonii* (Coult. & Rose) Cronq.

Pseudotsuga globosa Flous
= *P. menziesii* (Mirb.) Franco

Pseudotsuga taxifolia (Poir.) Britt. ex Sudw.
= *P. menziesii* (Mirb.) Franco

Psoralea castorea Wats.

Psoralea lanceolata Pursh var. *purshii* (Vail) Piper
= *P. lanceolata* var. *lanceolata*

Psoralea rafaclensis Jones
= *P. aromatica* Payson

Psoralea rafaclensis Jones var. *magna* Jones
= *P. aromatica* Payson

Psoralea stenophylla Rydb.
= *P. lanceolata* var. *stenophylla* (Rydb.) Toft & Welsh

Psoralea stenostachys Rydb.
= *P. lanceolata* var. *stenostachys* (Rydb.) Welsh

Ptelca ambigens Greene
= *P. trifoliata* ssp. *pallida* var. *pallida*

Ptelea baldwinii T. & G.
= *P. trifoliata* ssp. *pallida* (Greene) V.K. Bailey

Ptelea neglecta Greene
= *P. trifoliata* ssp. *pallida* var. *lutescens* (Greene) V.K. Bailey

Pterchiton occidentale Torr. & Frem. in Frem.
= *Atriplex canescens* (Pursh) Nutt.

Pteris aquilina L.
= *Pteridium aquilinum* (L.) Kuhn

Pteryxia hendersonii (Coult. & Rose) Math. & Const.
= *Cymopterus hendersonii* (Coult. & Rose) Cronq.

Pteryxia terebinthina (Hook.) Coult. & Rose
= *Cymopterus terebinthinus* (Hook.) T. & G.

Pteryxia terebinthina (Hook.) Coult. & Rose var. *calcarca* (Jones) Mathias
Syn: *Cymopterus calcarca* Jones = *C. terebinthinus* (Hook.) T. & G.

Ptilocalais macrolepis Rydb.
= *Microseris nutans* (Geyer) Schulz-bip

Puccinellia airoides (Nutt.) Wats. & Coult. in Gray
Syn: *Poa airoides* Nutt. = *P. nuttalliana* (Schult.) A.S. Hitchc.

Puccinellia lemmonii (Vasey) Scribn.
= Reporting error?

Pyrola chlorantha Swartz
= *P. virens* Schweigg

Pyrola picta Smith in Rees
= Reporting error?

Pyrola umbellata L.
= *Chimaphila umbellata* (L.) Bart.

Pyrola uniflora L.
= *Moneses uniflora* (L.) Gray

Pyrocoma cheiranthifolia Greene
= *Haplopappus clementis* (Rydb.) Blake

Pyrocoma clementis Rydb.
= *Haplopappus clementis* (Rydb.) Blake

Pyrocoma lapathifolia Greene
= *Haplopappus integrifolius* Gray?

Pyrocoma subcaesia Greene
= *Haplopappus clementis* (Rydb.) Blake

Pyrocoma uniflora (Hook.) Greene
= *Haplopappus uniflorus* (Hook.) T. & G.

Quercus eastwoodiae Rydb.
= *Q. gambelii* Nutt.

- Quercus stellata* var. *utahensis* DC.
 = *Q. gambelii* Nutt.
Quercus utahensis (A. DC.) Rydb.
 = *Q. gambelii* Nutt.
Ranunculus andersonii Gray var. *tenellus* Wats.
 = *R. juniperinus* Jones
Ranunculus orthorhynchus Hook. var. *alpinus* Wats.
 = *R. adoneus* var. *alpinus* (Wats.) L. Benson
Ranunculus repens L. var. *glabratus* DC.
 = *R. repens* var. *repens*
Ranunculus utahensis Rydb.
 = *R. inamoenus* var. *alpephilus* (A. Nels.) L. Benson
Ratibida columnaris authors, not (Sims) D. Don in Sweet
 = *R. columnifera* (Nutt.) Woot. & Standl.
Rhus cismontana Greene
 = *R. glabra* L.
Rhus nitens Greene
 = *R. glabra* L.
Rhus radicans L. var. *rydbergii* (Small) Rehder
 = *Toxicodendron rydbergii* (Small) Greene
Rhus rydbergii Small ex Rydb.
 = *Toxicodendron rydbergii* (Small) Greene
Rhus toxicodendron var. *rydbergii* (Small) Garrett
 = *Toxicodendron rydbergii* (Small) Greene
Rhus utahensis Goodding
 = *R. trilobata* var. *simplicifolia* (Greene) Barkley
Rhysopterus jonesii Coult. & Rose
 = *Cymopterus coulteri* (Jones) Mathias
Ribes cereum Dougl. var. *inebrians* (Lindl.) C.L. Hitchc.
 = *R. cereum* Dougl.
Ribes inebrians Lindl.
 = *R. cereum* Dougl.
Ribes lacustre (Pers.) Poir. in Lam. var. *lentum* Jones
 = *R. montigenum* McClatchie
Ribes mogollonicum Greene
 = *R. wolfii* Rothrock
Ribes petiolare Dougl.
 = *R. hudsonianum* Richards.
Riddellia tagetina var. *sparsiflora* Gray
 = *Psilostrophe sparsiflora* (Gray) A. Nels.
Rochelia patens Nutt.
 = *Hackelia patens* (Nutt.) Johnston.
Rorippa alpina (Wats.) Rydb.
 = *R. curvipes* var. *alpina* (Wats.) Stuckey
Rorippa armoracia (L.) A.S. Hitchc.
 = *Armoracia rusticana* Gaertn.
Rorippa curvisiliqua (Hook.) Bessey ex Britt.
 = *R. curvipes* Greene
Rorippa integra Rydb.
 = *R. curvipes* var. *integra* (Rydb.) Stuckey
Rorippa nasturtium-aquaticum (L.) Schinz & R. Keller
 = *Nasturtium officinale* R. Br. Syn: *Sisymbrium nasturtium-aquaticum* L.
Rorippa obtusa (Nutt.) Britt.
 = *R. curvipes* Greene
Rosa manca Greene
 = *R. woodsii* Lindl.
Rubus strigosus Michx.
 = *R. idaeus* ssp. *melanolasius* (Dieck.) Focke
Rudbeckia columnifera Nutt.
 = *Ratibida columnifera* (Nutt.) Woot. & Standl.
Rumex digyna L.
 = *Oxyria digyna* (L.) Hill
Rumex fueginus Phil.
 = *R. maritimus* L.
Rumex maritimus L. var. *athrix* St. John
 = *R. maritimus* L.
Rumex subalpina Jones
 = *R. pycnanthus* Rech. f.
Rumex triangulivalvis (Danser) Rech. f.
 = *R. salicifolius* Weinm.
Rumex utahensis Rech. f.
 = *R. salicifolium* Wein.
Salicornia rubra A. Nels.
 = *S. europaea* L.
Salicornia utahensis Tidestr.
 = *S. pacifica* var. *utahensis* (Tidestr.) Munz
Salix anglorum Cham. var. *antiplasta* Schneid.
 = *S. arctica* Pallas
Salix bebbiana Sarg. var. *perrostrata* (Rydb.) Schneid.
 = *S. bebbiana* Sarg.
Salix boothii Dorn
 = *S. myrtifolia* Anderss.
Salix caudata (Nutt.) Heller
 Syn: *S. pentandra* var. *caudata* Nutt. = *S. lasiandra* Benth.
Salix caudata (Nutt.) Heller var. *parvifolia* Ball
 = *S. lasiandra* Benth.
Salix lutea Nutt.
 = *S. rigida* Muhl.
Salix lutea Nutt. var. *platyphylla* Ball
 = *S. rigida* Muhl.
Salix melanopsis Nutt.
 = *S. exigua* ssp. *melanopsis* (Nutt.) Cronq.
Salix nivalis Hook.
 = *S. reticulata* L.
Salix pseudocordata (Anderss.) Rydb.
 = *S. myrtillifolia* Anderss.
Salix pseudolapponicum Seem. in Engler.
 = *S. glauca* L.
Salix subcoerulea Piper
 = *S. drummondiana* Barratt
Salsola hyssopifolia Pallas
 = *Bassia hyssopifolia* (Pallas) Kuntze
Salsola kali authors, not L.
 = *S. iberica* Sennen & Pau
Salvia carnosa Dougl. ex Greene
 = *S. dorrii* (Kellogg) Abrams
Sambucus glauca Nutt. in T. & G.
 = *S. caerulea* Raf.
Sambucus melanocarpa Gray
 = *S. racemosa* L.
Santolina suaveolens Pursh
 = *Chamomilla suaveolens* (Pursh) Rydb.
Saponaria segetalis Neck.
 = *Vaccaria pyramidata* Medicus
Saponaria vaccaria L.
 = *Vaccaria pyramidata* Medicus

- Saxifraga arguta* authors, not D. Don
= *S. odontoloma* Piper
- Saxifraga caespitosa* L. ssp. *exaratooides* var. *purpusii* Engler & Irmsch.
= *S. caespitosa* var. *minima* Blankinship
- Saxifraga oregona* Howell
= Reporting error?
- Schmaltzia affinis* Greene
= *Rhus trilobata* var. *simplicifolia* (Greene) Barkley
- Schoberia occidentalis* Wats.
= *Suaeda occidentalis* (Wats.) Wats.
- Schoenocrambe pinnata* Greene
= *S. linifolia* (Nutt.) Greene
- Scirpus olneyi* Gray
= *S. americana* Pers.
- Scirpus paludosus* A. Nels.
= *S. maritimus* var. *paludosus* (A. Nels.) Kukenthal
- Scirpus supinus* L.
= Reporting error?
- Sclerocactus whipplei* authors, not (Engelm. & Bigel.) Britt. & Rose
= *S. parviflorus* Clover & Jotter sens. lat.
- Scrophularia utahensis* Gandg.
= *S. lanceolata* Pursh?
- Scutellaria angustifolia* Pursh
= Reporting error?
- Sedum meehanii* Gray
= ? *S. lanceolatum* Torr.
- Sedum stenopetalum* authors, not Pursh
= *S. lanceolatum* Torr.
- Senecio ambrosioides* Rydb.
= *S. eremophilus* var. *kingii* (Rydb.) Greenm.
- Senecio aquariensis* Greenm.
= *S. streptanthifolius* Greene
- Senecio convallium* Greenm.
= *S. canus* Hooker
- Senecio incurvus* A. Nels.
= *S. spartioides* T. & G.
- Senecio jonesii* Rydb.
= *S. streptanthifolius* Greene
- Senecio kingii* Rydb.
= *S. eremophilus* var. *kingii* (Rydb.) Greenm.
- Senecio leonardii* Rydb.
= *S. streptanthifolius* Greene
- Senecio lugens* Richards. var. *hookeri* D.C. Eaton in Wats.
= *S. sphaerocephalus* Greene
- Senecio malmstenii* Blake in Tidestr.
= *S. streptanthifolius* Greene
- Senecio pammelii* Greenm.
= *S. streptanthifolius* Greene
- Senecio platylobus* Rydb.
= *S. streptanthifolius* Greene
- Senecio purshianus* Nutt.
= *S. canus* Hook.
- Senecio rubricaulis* var. *aphanactis* Greenm.
= *S. streptanthifolius* Greene
- Senecio uintahensis* (A. Nels.) Greenm.
= *S. multilobatus* T. & G.
- Senecio wardii* Greene
= *S. streptanthifolius* Greene
- Sesuvium sessile* Robins. in Gray
= *S. verracosum* Raf.
- Setaria lutescens* (Wiegel.) Hubbard
= *S. glauca* (L.) Beauv.
- Sicyos lobata* Michx.
= *Echinocyttis lobata* (Michx.) T. & G.
- Sida hederacea* (Dougl.) Torr. in Gray
= *Malvella leprosa* (Dougl.) Torr.
- Sidalcea crenulata* A. Nels.
= *S. neomexicana* var. *crenulata* (A. Nels.) C.L. Hitchc.
- Sieversia rossii* R. Br.
= *Geum rossii* (R. Br.) Ser.
- Sieversia scapoidea* A. Nels. in Coult. & Nels.
= *Geum rossii* (R. Br.) Ser.
- Silene drummondii* Hook.
= *Lychnis drummondii* (Hook.) Wats.
- Simapsis kaber* DC.
= *Brassica kaber* (DC.) Wheeler
- Sisymbrium elegans* (Jones) Payson
= *Thelypodiopsis elegans* (Jones) Rydb.
- Sisymbrium linifolium* Nutt. ex T. & G.
= *Schoenocrambe linifolia* (Nutt.) Greene
- Sisymbrium nasturtium-aquaticum* L.
= *Nasturtium officinale* R. Br.
- Sisyrinchium montanum* authors not Greene
= *S. idahoense* Bickn.
- Sisyrinchium occidentale* Bickn.
= *S. idahoense* Bickn.
- Sisyrinchium radicum* Bickn.
= *S. demissum* Greene
- Sisyrinchium sarmentosum* Suksd.
= Reporting error?
- Sisyrinchium segetum* Bickn.
= *S. idahoense* Bickn.
- Sitanion hansenii* (Scribn.) J.G. Sm.
= *Elysitanion hansenii* (Scribn.) Bowden Syn: *Elymus hansenii* Scribn.
- Sitanion insulare* J.G. Sm.
= *Agrositanion saxicola* (Scribn. & Sm.) Bowden
- Sitanion longifolium* J.G. Sm.
= *S. hystris* var. *brevifolium* (J.G. Sm.) C.L. Hitchc.
- Solidago altissima* L.
= *S. canadensis* L.
- Solidago decumbens* Greene
= *S. spatulata* DC.
- Solidago elongata* Nutt.
= *S. canadensis* L.
- Solidago garrettii* Rydb.
= *S. sparsiflora* Gray
- Solidago petradoria* Blake
= *Petradoria pumila* (Nutt.) Greene
- Solidago radulina* Rydb.
= *S. nana* Nutt.
- Solidago trinervata* Greene
= *S. sparsiflora* Gray
- Sonchus asper* (L.) All. var. *glanduliferus* Garrett
= *S. asper* (L.) Hill

- Sonchus biennis* Moench
 = *Lactuca biennis* (Moench) Fern.
Sonchus ludovicianus Nutt.
 = *Lactuca ludoviciana* (Nutt.) Riddell
Sophia leptostylis Rydb.
 = *Descurainia californica* (Gray) Schulz
Sophora kentukea Dum.-Cour.
 = *Cladrastis kenutkea* (Dum.-Cour.) Rudd
Sophora sericea Nutt.
 = *S. nuttalliana* Turner
Sorghum vulgare authors, not Pers.
 = *S. bicolor* (L.) Moench
Specularia perfoliata (L.) DC.
 = *Triodanis perfoliata* (L.) Niew.
Spergularia salina J. & C. Presl
 = *S. marina* (L.) Griseb.
Sphaeralcea digitata authors, not (Greene) Rydb.
 = *S. grossulariifolia* (H. & A.) Rydb.
Sphaeralcea subrhomboidea Rydb.
 = *S. munroana* (Dougl.) Spach
Sphaerostigma utahense Small
 = *Camissonia boothii* ssp. *alysoides* (H. & A.) Raven
Sphenopholis pallens (Spreng.) Scribn.
 = *S. obtusata* (Michx.) Scribn.
Spiraea caespitosa Nutt. in T. & G.
 = *Petrophytum caespitosum* (Nutt.) Rydb.
Spiraea caespitosa Nutt. in T. & G. var. *clatior* Wats.
 = *Petrophytum caespitosum* (Nutt.) Rydb.
Spiraea dumosa Nutt. ex Hook.
 = *Holodiscus dumosus* (Nutt.) Heller
Sporobolus asperifolius Nees. & Mey.
 = *Muhlenbergia asperifolia* (Nees & Mey.) Parodi
Spraguea umbellata Torr.
 = *Calyptridium umbellatum* (Torr.) Greene
Stachys asperrima Rydb.
 = *S. palustris* L.
Stachys pilosa Nutt.
 = *S. palustris* L.
Stanleya albescentis Jones
 = Reporting error?
Stanleya canescens Rydb.
 = *S. pinnata* var. *pinnata*
Statice sinuata L.
 = *Limonium sinuatum* (L.) Mill.
Stenotus falcatus Rydb.
 = *Haplopappus acaulis* var. *glabratus* (D.C. Eaton) Hall
Stenotus latifolius A. Nels.
 = *Haplopappus acaulis* var. *glabratus* (D.C. Eaton) H.M. Hall
Stipa columbiana Macoun
 = *S. nelsonii* Scribn.
Stipa hymenoides R. & S.
 = *Oryzopsis hymenoides* (R. & S.) Riker
Stipa mormonum Mez.
 = *S. arida* Jones
Stipa parishii var. *depauperata* Jones
 = *S. coronata* var. *depauperata* (Jones) A.S. Hitchc.
Stipa williamsii Scribn.
 = *S. columbiana* Macoun
Suaeda depressa (Pursh) Wats.
 = *S. calceoliformis* (Hook.) Moq.
Suaeda fruticosa Wats.
 = *S. torreyana* Wats.
Swainsonia salsula (Pallas) Taub. in Engelm. & Prantl
 = *Sphaerophysa salsula* (Pallas) DC.
Swertia fritillaria Rydb.
 = *S. perennis* L.
Symphoricarpos utahensis Rydb.
 = *S. oreophilus* Gray
Symphoricarpos vaccinioides Rydb.
 = *S. oreophilus* Gray
Synthesis laciniata (Gray) Rydb. ssp. *ibahpensis* Pennell
 = *S. laciniata* (Gray) Rydb.
Synthesis pinnatifida Wats. var. *laciniata* Gray
 = *S. laciniata* (Gray)
Talinum pygmaeum Gray
 = *Lewisia pygmaea* (Gray) Robins.
Tamarix gallica authors, not L.
 = *T. ramosissima* Ledeb.
Tamarix pentandra authors, not Pall.
 = *T. ramosissima* Ledeb.
Tanacetum diversifolium D.C. Eaton
 = *Sphaeromeria diversifolia* Rydb.
Tanacetum nuttallii T. & G.
 = *Sphaeromeria argentea* Nutt.
Tellima parviflora Hook.
 = *Lithophragma parviflora* (Hook.) Nutt. ex T. & G.
Tetradymia linearis Rydb.
 = *T. canescens* DC.
Tetradymia spinosa H. & A. var. *longispina* Jones
 = *T. axillaris* var. *longispina* Jones
Tetranneuris punctata A. Nels.
 = *Hymenoxys acaulis* var. *caespitosus* (A. Nels.) Parker
Thalictrum duriusculum Greene
 = *T. alpinum* L.
Thelypodium elegans Jones
 = *Thelypodopsis elegans* (Jones) Rydb.
Thelypodium lilacinum Greene
 = *T. integrifolium* var. *integrifolium*
Thelypodium macropetalum Rydb.
 = *T. sagittatum* var. *sagittatum*
Thelypodium ovalifolium Rydb.
 = *T. sagittatum* var. *ovalifolium* (Rydb.) Welsh & Reveal
Thelypodium palmeri Rydb.
 = *T. sagittatum* var. *ovalifolium* (Rydb.) Welsh & Reveal
Thelypodium suffrutescens Rollins in Graham
 = *Glaucocarpum suffrutescens* (Rollins) Rollins
Thelypodium utahense Rydb.
 = *Caulanthus lasiophyllus* var. *utahensis* (Rydb.) Jeps.
Thelypodium wrightii Gray var. *tenellum* Jones
 = *T. laxiflorum* Al-Shebaz
Thlaspi alpestre L.
 = *T. montanum* L.
Thlaspi fendleri Gray var. *tenuipes* Maguire
 = *T. montanum* var. *montanum*

- Thlaspi prolixum* A. Nels.
= **T. montanum** var. **montanum**
- Thysanocarpus trichocarpus* Rydb.
= **T. curvipes** Hook.
- Tiquilia canescens* (DC.) A. Richards.
Syn: *Coldenia canescens* DC.
- Tissa salina* (J. & C. Presl) Britt.
= **Spergularia marina** (L.) Griseb. Syn: *Spergularia salina* J. & C. Presl
- Tithonia argophylla* D.C. Eaton
= **Enceliopsis argophylla** (D.C. Eaton) A. Nels.
- Townsendia arizonica* Gray
= **T. incana** Nutt.
- Townsendia dejecta* A. Nels.
= **T. montana** var. **montana**
- Townsendia florifer* (Hook.) Gray var. *communis* Jones
= **T. florifer** (Hook.) Gray
- Townsendia incana* Nutt. var. *prolixa* Jones
= **T. strigosa** Nutt.
- Townsendia mensana* Jones var. *jonesii* Beaman
= **T. jonesii** (Beaman) Reveal
- Townsendia scapigera* var. *ambigua* Gray
= **T. florifer** (Hook.) Gray
- Townsendia watsonii* Gray
= **T. florifer** (Hook.) Gray
- Toxicodendron longipes* Greene
= **T. rydbergii** (Small) Greene
- Toxicodendron radicans* var. *rydbergii* (Small) Erskine
= **T. rydbergii** (Small) Greene
- Tradescantia laramiensis* Goodding
= **T. occidentalis** (Britt.) Smyth
- Tradescantia scopulorum* Rose
= **T. occidentalis** (Britt.) Smyth
- Tridens pilosus* (Buckl.) A.S. Hitchc.
= **Erioneuron pilosum** (Buckley) Nash
- Tridens pulchellus* (H.B.K.) A.S. Hitchc.
= **Erioneuron pulchellum** (H.B.K.) Tateoka
- Trifolium confusum* Rydb.
= **T. longipes** var. **pygmaeum** Gray
- Trifolium inequale* Rydb.
= **T. parryi** var. **montanense** (Rydb.) Welsh
- Trifolium longipes* Nutt. var. *brachypus* Wats.
= **T. longipes** var. **pygmaeum** Gray
- Trifolium uintense* Rydb.
= **T. dasyphyllum** var. **uintense** (Rydb.) Welsh
- Trifolium villiferum* House
= **T. eriocephalum** var. **villiferum** (House) Martin
- Triglochin maritima* L. var. *debile* Jones
= **T. concinna** var. **debile** (Jones) Howell
- Triodia mutica* (Torr.) Benth. ex Wats.
= **Tridens muticus** (Torr.) Nash
- Triodia pilosa* (Buckl.) Merr.
= **Erioneuron pilosum** (Buckl.) Nash
- Triodia pulchella* (H.B.K.)
= **Erioneuron pulchellum** (H.B.K.) Tateoka
- Tripolium angustum* Lindl. in Hook.
= **Aster brachyactis** Blake
- Tripterocalyx pedunculatus* (Jones) Standl.
Syn: *Abronia micrantha* var. *pedunculata* Jones = **T. micranthus** (Torr.) Hook.
- Tripterocalyx wootonii* Standl.
= **T. carnea** var. **wootonii** (Standl.) Galloway
- Typha angustifolia* authors, not L.
= **T. domingensis** Pers.
- Urtica breweri* Wats.
= **U. serra** Blume
- Urtica gracilis* Ait.
= **U. dioica** ssp. **gracilis** (Ait.) Seland.
- Vaccaria segetalis* (Neck.) Garcke ex Aschers
= **V. pyramidata** Medicus
- Vaccinium globulare* Rydb.
= **V. membranaceum** Dougl. sensu Utah
- Valeriana capitata* Pallas ssp. *pubicarpa* (Rydb.) F.G. Mey.
= **V. acutiloba** var. **pubicarpa** (Rydb.) Cronq.
- Valerianella macrocera* (T. & G.) Gray
= **Plectritis macrocera** T. & G.
- Valeriana micrantha* E. Nels.
= **V. occidentalis** Heller
- Valeriana obovata* (Nutt.) R. & S.
= **V. edulis** Nutt.
- Valeriana puberulenta* Rydb.
= **V. acutiloba** var. **pubicarpa** (Rydb.) Cronq.
- Valeriana pubicarpa* Rydb.
= **V. acutiloba** var. **pubicarpa** (Rydb.) Cronq.
- Valeriana utahensis* Gandg.
= **V. acutiloba** var. **pubicarpa** (Rydb.) Cronq.
- Verbena bracteosa* Michx.
= **V. bracteata** Lag. & Rodr.
- Verbena macdougalii* Heller
= **Verbena gooddingii** Brig.
- Verbesina scaposa* Jones
= **Enceliopsis nutans** (Eastw.) A. Nels.
- Vicia exigua* Nutt. in T. & G.
= **V. ludoviciana** Nutt.
- Viguiera annua* (Jones) Blake
= **Heliomeris annua** (Jones) Yates
- Viguiera ciliata* (Robins. & Greenm.) Blake
Syn: *Gymnolomia hispida* var. *ciliata* Robins. & Greenm.
= **Heliomeris hispida** (Gray) Cockerell
- Viguiera multiflora* (Nutt.) Blake
= **Heliomeris multiflora** Nutt.
- Viguiera multiflora* (Nutt.) Blake var. *nevadensis* (A. Nels.) Blake
= **Helianthus multiflora** var. *nevadensis* (A. Nels.) Yates
- Viguiera soliceps* Barneby
= **Heliomeris soliceps** (Barneby) Yates
- Vilfa depauperata* Torr. ex Hook. var. *filiformis* Thurb. in Wats.
= **Muhlenbergia filiformis** (Thurb.) Rydb.
- Viola beckwithii* T. & G. var. *cachensis* C.P. Sm.
= **V. beckwithii** T. & G.
- Viola bellidifolia* Greene ssp. *valida* Baker
= **V. adunca** J.E. Sm.
- Viola bonnevillensis* Cottam
= **V. beckwithii** T. & G.

- Viola charlestonensis* Baker & Clausen
 = *V. purpurea* var. *charlestonensis* (Baker & Clausen) Welsh & Reveal
Viola clauseniana Baker
 = *V. nephrophylla* Greene
Viola mamillata Greene
 = *V. adunca* J.E. Sm.
Viola montanensis Rydb.
 = *V. adunca* J.E. Sm.
Viola nuttallii Pursh var. *major* Hook.
 = *V. nuttallii* Pursh
Viola nuttallii Pursh var. *praemorsa* (Dougl.) Wats.
 = *V. nuttallii* Pursh
Viola nuttallii Pursh var. *vallicola* (A. Nels.) Hitchc. in St. John
 = *V. nuttallii* Pursh
Viola oxysepala Greene
 = *V. adunca* J.E. Sm.
Viola praemorsa Dougl. ex Lindl.
 = *V. nuttallii* Pursh
Viola tidestromii Greene
 = *V. adunca* J.E. Sm.
Viola utahensis Baker & Clausen
 = *V. purpurea* Kellogg
Viola vallicola A. Nels.
 = *V. nuttallii* Pursh
Whipplea utahensis Wats.
 = *Fendlerella utahensis* (Wats.) Heller
Wyomingia vivax A. Nels.
 = *Erigeron utahensis* var. *sparsifolius* (Eastw.) Cronq.
Xanthium saccharatum Wallr.
 = *X. strumarium* L.
Xylophacos aragaloides Rydb.
 = *Astragalus amphioxys* var. *amphioxys*
Xylophacos marianus Rydb.
 = *Astragalus marianus* (Rydb.) Barneby
Xylophacos mcdiui Rydb.
 = *Astragalus eurekensis* Jones
Xylophacos melanocalyx Rydb.
 = *Astragalus amphioxys* var. *amphioxys*
Xylophacos uintensis Rydb.
 = *Astragalus argophyllus* var. *argophyllus*
Xylorhiza lanceolata Rydb.
 = *X. tortifolia* var. *tortifolia*
Yucca angustissima Engelm. var. *kanabensis* (McKelvey) Reveal
 = *Y. kanabensis* McKelvey
Yucca gilbertiana (Trel.) Rydb.
 Syn: *Y. harrimaniae* var. *gilbertiana* Trel. = *Y. harrimaniae* Trel.
Yucca harrimaniae Trel. var. *gilbertiana* Trel.
 = *Y. harrimaniae* Trel.
Yucca smalliana Fern.
 = *Y. filamentosa* var. *smalliana* (Fern.) Ahles
Yucca standleyi McKelvey
 = *Y. bailey* Woot. & Standl.
Zauschneria garrettii A. Nels.
 = *Epilobium canum* (Greene) Raven
Zauschneria garrettii A. Nels.
 = *Epilobium canum* (Greene) Raven
Zigadenus gramineus Rydb.
 = *Z. venenosus* Wats.

REVISED CHECKLIST OF THE VASCULAR PLANTS OF BRYCE CANYON NATIONAL PARK, UTAH

Hayle Buchanan¹ and Robert Graybosch²

ABSTRACT.— Prior to 1960, when the senior author wrote a dissertation on the plant ecology of the Paunsaugunt Plateau forests of Bryce Canyon National Park, relatively little plant taxonomic work had been done in the area. A checklist was prepared in 1971 that included 218 species of higher plants. During the field seasons 1978, 1979, and 1980, additional plants were collected during a second plant community study of the forests. The junior author spent the summer of 1980 at the park collecting plants in additional plant communities and organizing the herbarium collection. This checklist includes the additional species collected and updates the nomenclature of the vascular plants presently known to occur within the boundaries of Bryce Canyon National Park.

Bryce Canyon National Park occupies 35,240 acres (55.06 square miles) along the southeastern edge of the Paunsaugunt Plateau in Garfield and Kane counties in southern Utah. The elevation ranges from 2027 m (6650 ft) near the town of Tropic to 2775 m (9105 ft) at Rainbow Point. The Paunsaugunt Plateau is approximately 30 miles long by 10 miles wide, occupying a position midway between 37 degrees and 38 degrees north latitude 10 miles west of the 112th meridian. The annual precipitation at park headquarters is 16.56 inches. May and June are the driest months of the year with .94 and .60 inches of precipitation. August is the wettest month of the year with 2.35 inches precipitation, due to thunderstorms. Snowfall from November through March provides most of the annual precipitation.

The checklist includes 446 species of vascular plants known to occur within the boundaries of Bryce Canyon National Park. It should not be considered all inclusive, inasmuch as additional species will undoubtedly be discovered. It is, rather, the state of knowledge as of August 1980. The following have served as authorities of nomenclature: monocotyledons, Cronquist et al. (1977); Fabaceae, Welsh (1978); Brassicaceae, except *Erysimum*, Welsh and Reveal (1977); lower vascular plants, gymnosperms and remainder of the dicotyledons, Holmgren and Reveal

(1966), with the exception of the genera *Heterotheca*, *Solidago*, and *Chrysothamnus*, where the nomenclature of Welsh and Moore (1973) was employed.

Welsh, Atwood, and Murdock (1978) cited numerous collections from Bryce Canyon. Some species listed were not located in the field by the present authors. These are included in the checklist and are listed as follows:

Erigeron abajoensis Cronq.
E. compositus Pursh
E. vagus Pays.
Leucelene cricoides (Torr.) Greene
Physaria newberryi Gray
Thelypodium sagittatum (Nutt.) Endl. var. *ovalifolium* (Rydb.) Welsh and Reveal
Arenaria nuttallii S. Wats.
Carex eleocharis L. H. Bailey
Lathyrus brachycalyx Rydb. var. *zionis* (C. L. Hitchc.) Welsh
Lupinus X alpestris A. Nels.
Linanthastrum nuttallii (Gray) Ewan
Phlox hoodii Richards
Polemonium viscosum Nutt.

Due to the local edaphic and topographic features, the Bryce Canyon flora is rich in rare and endemic plants. The following list includes those plants cited by Welsh (1979) whose presence in Bryce Canyon has been documented by the authors, or, in the case of *Erigeron abajoensis*, other investigators.

Erigeron abajoensis Cronq.
Heterotheca jonesii (Blake) Welsh and Atwood

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Townsendia minima Eastw.
Cryptantha ochroleuca Higgins
Draba subalpina Goodmn. and Hitchc.
Lesquerella rubicundula Rollins
Silene petersonii Maguire var. *minor* C. L. Hitchc. & Maguire
Psoralea pariensis Welsh & Atwood
Castilleja revealii N. Holmgren
Penstemon bracteatus Keck.

Erigeron abajoensis was cited by Welsh et al. (1978). We have not seen it in the field. According to Welsh (1979), *Heterotheca jonesii* was known from one surviving population. The Bryce Canyon collection (Graybosch, 924) is, therefore, a significant extension of the range of this rare plant. One population was located on a sandy outcrop of the Kaiparowits formation in Bridge Canyon at an elevation of 2438 m (8000 ft). Identical habitat is available throughout the southern half of the park; yet no other populations have been located. The site is traversed by a hiking trail, presenting the danger of trampling.

Townsendia minima, *Draba subalpina*, and *Lesquerella rubicundula* are common wherever exposed limestone exists. Their "threatened or endangered" status might need reconsideration. *Cryptantha ochroleuca* has been observed near East Creek, Inspiration Point, and below Bryce Point. Populations are small and Welsh's (1979) suggestion that the species be regarded as endangered is certainly justifiable. *Psoralea pariensis* is represented only by a few small, scattered populations along the rim of the Paunsaugunt Plateau.

Silene petersonii var. *minor* and *Penstemon bracteatus* are known in the park only from the main amphitheater (herein defined as that portion of the park bordered by Bryce Point on the south, Tropic and Little Henderson Canyons on the north, and from the rim of the Paunsaugunt Plateau to the interface of the Wasatch formation with the underlying Kaiparowits formation) and from outcrops of the Wasatch limestone bordering East Creek. Populations consist of only a few scattered individuals. *Castilleja revealii* is the rarest of these plants, known only from the main amphitheater. Maintenance of the few populations is critical because, according to Welsh (1979), the Reveal paintbrush is known only from Bryce Canyon.

Cymopterus minimus, *Phlox gladiiformis*, and *Eriogonum aretioides* are rare plants known from areas close to Bryce Canyon (Cedar Breaks and/or Red Canyon). Since these sites are similar to Bryce Canyon both edaphically and topographically, one might expect to find these species in Bryce Canyon. Despite extensive search, they have not been located in the Park, thereby making protection of the existing populations all the more vital.

In the paper "The Flora of Great Basin Mountain Ranges: Diversity, Sources, and Dispersal Ecology" the flora of Bryce Canyon, based on a 1971 checklist of the national park, was used as a "continental" flora. Of all the continental floras used in the paper, that of Bryce Canyon was considered the most depauperate. The equation: no. of species = $295.4 (\log \text{area})^{0.11}$ predicted 460 species for Bryce Canyon with 55.06 square miles of area, but only 218 species were reported. This new checklist includes 446 species, which closely approximates the predicted number of species.

THE VASCULAR PLANTS OF BRYCE CANYON NATIONAL PARK

Aceraceae

1. *Acer glabrum* Torr. (Rocky Mountain maple).
2. *A. grandidentatum* Nutt. (bigtoothed maple).

Amaranthaceae

3. *Amaranthus graecizans* L. (tumbleweed amaranth).

Anacardiaceae

4. *Rhus trilobata* Nutt. (squawbush).

Apiaceae

5. *Cicuta douglasii* (DC.) Coult. & Rose (Douglas water hemlock).
6. *Cymopterus purpureus* S. Wats. (purple biscuit-root).
7. *Ligusticum porteri* Coult. & Rose (ligusticum).
8. *Lomatium minimum* Mathias (Bryce Canyon lomatium).
9. *Lomatium nuttallii* (Gray) Macbr. (desert parsley).
10. *Cymopterus lemmonii* (Coult. & Rose) Dom. (pseudocymopterus).

Apocynaceae

11. *Apocynum androsaemifolium* L. (dogbane).

Asclepidaceae

12. *Asclepias asperula* (Decne.) Woodson (milkweed).

Asteraceae (Compositae)

13. *Achillea millefolium* L. (yarrow).
14. *Agoseris aurantiaca* (Hook.) Greene var. *aurantiaca* (mountain dandelion).

15. *A. aurantiaca* (Hook.) Greene var. *purpurea* (Gray) Cronq. (mountain dandelion).
 16. *A. glauca* (Pursh). D. Dietl. var. *parviflora* (Nutt.) Rydb. (mountain dandelion).
 17. *Antennaria dimorpha* (Nutt.) T. & G. (low pussytoes).
 18. *A. parvifolia* Nutt. (pussytoes).
 19. *A. rosea* Greene (rose pussytoes).
 20. *A. rosulata* Rydb. (pygmy pussytoes).
 21. *Arnica chamissonis* Less. (woolly arnica).
 22. *A. cordifolia* Hook. (heartleaf arnica).
 23. *Artemisia arbuscula* Nutt. var. *nova* (A. Nels.) Cronq. (black sage).
 24. *A. carruthii* Wood (Carruth sage).
 25. *A. frigida* Willd. (fringed sage).
 26. *A. ludoviciana* Nutt. (Louisiana sage).
 27. *A. pygmaea* Gray (pygmy sage).
 28. *A. tridentata* Nutt. (big sage).
 29. *Aster chilensis* Nees (aster).
 30. *A. eatonii* (Gray) Howell (bog aster).
 31. *A. glaucodes* Blake (pale aster).
 32. *A. integrifolius* Nutt. (thickstem aster).
 33. *A. occidentalis* (Nutt.) Torr. & Gray (western aster).
 34. *Balsamorhiza sagittata* (Pursh) Nutt. (arrowleaf balsamroot).
 35. *Brickellia oblongifolia* Nutt. (bricklebrush).
 36. *Centaurea repens* L. (Russian knapweed).
 37. *Chaenactis douglasii* (Hook.) Hook. & Arn (chaenactis).
 38. *Chrysanthamnus depressus* Nutt. (dwarf rabbitbrush).
 39. *C. linifolius* Greene (broadleaf rabbitbrush).
 40. *C. nauseosus* (Pall.) Britton var. *graveolens* (Nutt.) Hall (rubber rabbitbrush).
 41. *C. parryi* (Gray) Greene (Parry rabbitbrush).
 42. *C. vaseyi* (Gray) Greene (rabbitbrush).
 43. *C. viscidiflorus* (Hook.) Nutt. var. *viscidiflorus* (rabbitbrush).
 44. *Cirsium arizonicum* (Gray) Petrak (Arizona thistle).
 45. *C. canovirens* (Rydb.) Petrak (thistle).
 46. *C. nidulum* (Jones) Petrak (thistle).
 47. *C. pulchellum* (Greene) Woot. & Standl. (purple thistle).
 48. *C. undulatum* (Nutt.) Spreng (wavyleaf thistle).
 49. *Crepis intermedia* Gray (hawk's beard).
 50. *C. occidentalis* Nutt. (western hawk's beard).
 51. *C. runcinata* (James) T & G var. *glauca* (Nutt.) Babcock & Stebbins (dandelion hawk's beard).
 52. *Erigeron abajoensis* Cronq. (abajo daisy).
 53. *E. canus* Gray (fleabane).
 54. *E. compositus* Pursh (dwarf daisy).
 55. *E. divergens* T & G (spreading daisy).
 56. *E. eatoni* Gray (Eaton fleabane).
 57. *E. flagellaris* Gray (trailing fleabane).
 58. *E. pumilus* Nutt. ssp. *concinoides* Cronq. (low fleabane).
 59. *E. simplex* Greene (rock daisy).
 60. *E. speciosus* (Lindl.) DC var. *macranthus* (Nutt.) Cronq. (largeleaf fleabane).
 61. *E. ursinus* D.C. Eaton (Bear River fleabane).
 62. *Erigeron vagus* Pays. (fleabane).
 63. *Grindelia squarrosa* (Pursh) Dunal (gumweed).
 64. *Gutierrezia sarothrae* (Pursh) Britt. & Rusby (snake-weed).
 65. *Haplopappus armerioides* (Nutt.) Gray (gold-enweed).
 66. *Helianthella uniflora* (Nutt.) T & G (helianthella).
 67. *Helianthus annuus* L. (sunflower).
 68. *Heterotheca jonesii* (Blake) Welsh & Atwood (Jones goldenaster).
 69. *H. villosa* (Pursh) Shinnars (goldenaster).
 70. *Hymenopappus filifolius* Hook. var. *cinereus* (Rydb.) I. M. Johnston (hymenopappus).
 71. *H. filifolius* Hook. var. *lugens* (Greene) Jeps. (hymenopappus).
 72. *Hymenoxys acaulis* (Pursh) Parker (stemless hymenoxys).
 73. *H. richardsonii* (Hook.) Cockerell (Colorado rubberweed).
 74. *Iva axillaris* Pursh (sumpweed).
 75. *Lactuca pulchella* (Pursh) DC (wild lettuce).
 76. *L. serriola* L. (prickly lettuce).
 77. *Leucclene ericoides* (Torr.) Greene (petite aster).
 78. *Lygodesmia grandiflora* (Nutt.) T. & G (rush pink).
 79. *L. spinosa* Nutt. (thorn skeletonweed).
 80. *Machaeranthera canescens* (Pursh) Gray (hoary machaeranthera).
 81. *M. grindelioides* (Nutt.) Shinnars (rayless goldenweed).
 82. *M. linearis* Greene (false aster).
 83. *Petradoria pumila* (Nutt.) Greene (rock goldenrod).
 84. *Senecio atratus* Greene (black groundsel).
 85. *S. cymbalarioides* Buek (cleftleaf groundsel).
 86. *S. multilobatus* Torr. & Gray (groundsel).
 87. *S. spartioides* T & G (broom groundsel).
 88. *Solidago spatulata* DC (mountain goldenrod).
 89. *S. missouriensis* Nutt. (Missouri goldenrod).
 90. *S. parryi* (Gray) Greene (Parry goldenrod).
 91. *S. sparsiflora* Gray (goldenrod).
 92. *Stephanomeria tenuifolia* (Torr.) Hall (wirelettuce).
 93. *Tanacetum nuttallii* T & G (rock tansy).
 94. *Taraxacum officinale* Weber (dandelion).
 95. *Tetradymia canescens* DC (horsebrush).
 96. *Townsendia excapa* (Richards) Porter (stemless townsendia).
 97. *T. incana* Nutt. (hoary townsendia).
 98. *T. minima* Eastw. (least townsendia).
 99. *Tragapogon dubius* Scop. (goatsbeard).
 100. *Verbesina encelioides* (Cav.) Benth. & Hook. (crownbeard).
 101. *Viguiera multiflora* (Nutt.) Blake (showy goldeneye).
- Berberidaceae**
102. *Berberis fremontii* Torr. (Fremont barberry).
 103. *B. repens* Lindll. (creeping barberry).
- Betulaceae**
104. *Betula occidentalis* Hook. (water birch).
- Boraginaceae**
105. *Cryptantha abata* I. M. Johnston (cryptantha or cat's eye).
 106. *C. bakeri* (Greene) Payson (cryptantha or cat's eye).
 107. *C. confertifolia* (Greene) Payson (cryptantha or cat's eye).
 108. *C. fendleri* (Gray) Greene (cryptantha or cat's eye).
 109. *C. flava* (Nels.) Payson (cryptantha or cat's eye).
 110. *C. fulvocanescens* (Gray) Payson (cryptantha or cat's eye).

111. *C. humilis* (Greene) Payson (cryptantha or cat's eye).
112. *C. jamesii* (Torr.) Payson (cryptantha or cat's eye).
113. *C. ochroleuca* Higgins (cryptantha or cat's eye).
114. *C. setosissima* (Gray) Payson (cryptantha or cat's eye).
115. *Lappula redowskii* (Hornem.) Greene (stickseed).
116. *Lithospermum incisum* Lehm. (gromwell).
117. *L. multiflorum* Torr. (puccoon).

Brassicaceae (Cruciferae)

118. *Arabis fendleri* (S. Wats.) Greene (rockcress).
119. *A. holboellii* Hornem. (rockcress).
120. *A. pendulina* Greene (rockcress).
121. *Capsella bursa-pastoris* (L.) Medic (shepherd's purse).
122. *Caulanthus crassicaulis* (Torr.) S. Wats. (wild cabbage).
123. *Conringia orientalis* (L.) Dumort (haresear).
124. *Descurainia obtusa* (Greene) O. E. Schulz (tansy mustard).
125. *D. richardsonii* (Sweet) O. E. Schulz (tansy mustard).
126. *D. sophia* (L.) Webb (tansy mustard).
127. *Draba subalpina* Goodman & Hitchc. (subalpine whitlograss).
128. *Erysimum capitatum* (Dougl.) Greene (western wallflower).
129. *E. inconspicuum* (S. Wats.) MacMill (little wallflower).
130. *Lepidium densiflorum* Schrad. (prairie pepperweed).
131. *L. montanum* Nutt. (mountain pepperweed).
132. *Lesquerella intermedia* (S. Wats.) Heller (bladderpod).
133. *L. kingii* S. Wats. var. *parvifolia* (Maguire & Holmgren) Welsh & Reveal (bladderpod).
134. *L. rubicundula* Rollins (Bryce bladderpod).
135. *Malcolmia africana* (L.) R. Br. (African mustard).
136. *Physaria chambersii* Rollins (twinpod).
137. *P. newberryi* Gray (twinpod).
138. *Sisymbrium linifolium* Nutt. (tumblemustard).
139. *Stanleya pinnata* (Pursh) Britton (prince's plume).
140. *Streptanthus cordatus* Nutt. (twistflower).
141. *Thelypodium sagittatum* (Nutt.) Endl. var. *ovalifolium* (Rydb.) Welsh & Reveal (thelypody).
142. *Thlaspi arvense* L. (field pennycress).

Cactaceae

143. *Opuntia erinacea* Engelm. (pricklypear).
144. *Pediocactus simpsonii* Engelm. (echinocactus).

Campanulaceae

145. *Campanula parryi* Gray (Parry bellflower).
146. *C. rotundifolia* L. (bluebell).

Capparidaceae

147. *Cleome lutea* Hook. (yellow beeplant).

Caprifoliaceae

148. *Sambucus cocculea* Raf. (elderberry).
149. *Symphoricarpos oreophilus* Gray var. *utahensis* (Rydb.) A. Nels. (snowberry).

Caryophyllaceae

150. *Arenaria fendleri* A. Gray (sandwort).
151. *A. nuttallii* Pax (sandwort).
152. *Lychnis drummondii* (Hook.) S. Wats. (campion).

153. *Paronychia sessiliflora* Nutt. (creeping nailwort).
154. *Silene petersonii* Maguire var. *minor* C. L. Hitchc. & Maguire (Red Canyon catchfly).
155. *Stellaria jamesiana* Torr. (chickweed).
156. *S. longipes* Goldie (starwort).

Celastraceae

157. *Pachistima myrsinites* (Pursh) Raf. (mountain lover).

Chenopodiaceae

158. *Atriplex canescens* (Pursh) Nutt. (four-winged saltbrush).
159. *A. tridentata* Kuntze (saltbrush).
160. *Chenopodium atrovirens* Rydb. (goosefoot).
161. *C. incanum* (S. Wats.) Heller (goosefoot).
162. *C. leptophyllum* Nutt. (slimleaf goosefoot).
163. *Eurotia lanata* (Pursh) Moq. (winterfat).
164. *Salsola iberica* Senner & Pau (Russian thistle).

Convolvulaceae

165. *Convolvulus arvensis* L. (field bindweed).

Cornaceae

166. *Cornus stolonifera* Michx. (redosier dogwood).

Cupressaceae

167. *Juniperus communis* L. (common juniper).
168. *J. osteosperma* (Torr.) Little (Utah juniper).
169. *J. scopulorum* Sarg. (Rocky Mountain juniper).

Cyperaceae

170. *Carex athrostachrya* Olney (slender-beaked sedge).
171. *C. aurea* Nutt. (golden sedge).
172. *C. canescens* L. (sedge).
173. *C. douglasii* Boott (Douglas sedge).
174. *C. eleocharis* L. H. Bailey (needleleaf sedge).
175. *C. microptera* Mke. (smallwing sedge).
176. *C. nebraskensis* Dewey (Nebraska sedge).
177. *C. oederi* Retz. (subalpine sedge).
178. *C. praegracilis* W. Boott (sedge).
179. *C. rossii* Boott (Ross sedge).
180. *C. rostrata* Stokes (beaked sedge).
181. *Eleocharis pauciflorus* (Lightf.) Link (spike-rush).
182. *E. rostellata* (Torr.) Torr. (beaked spike-rush).
183. *Scirpus americanus* Pers. (American bullrush).

Elaeagnaceae

184. *Shepherdia argentea* (Pursh) Nutt. (silver buffaloberry).
185. *S. canadensis* (L.) Nutt. (russet buffaloberry).
186. *S. rotundifolia* Parry (roundleaf buffaloberry).

Equisetaceae

187. *Equisetum arvense* L. (field horsetail).
188. *E. laevigatum* A. Br. (smooth horsetail).

Ericaceae

189. *Arctostaphylos patula* Greene (green leaf manzanita).
190. *A. uva-ursi* (L.) Spreng. (bearberry).

Euphorbiaceae

191. *Euphorbia fendleri* T & G (spurge).
192. *E. hurida* Engelm. (spurge).
193. *E. robusta* (Engelm.) Small (robust spurge).

Fabaceae

194. *Astragalus agrestis* Dougl. ex G. Don. (milkvetch).
195. *A. amphioxys* Gray (crescent milkvetch).

196. *A. argophyllus* Nutt. ex T & G var. *panguicensis* (M. E. Jones) M. E. Jones (silverleafed milkvetch).
197. *A. bisulcatus* (Hook.) Gray (two-grooved milkvetch).
198. *A. calycosus* Torr. ex S. Wats. (Torrey milkvetch).
199. *A. convallarius* Greene (lesser rushy milkvetch).
200. *A. hallii* Gray var. *fallax* (Wats.) Barneby (Hall milkvetch).
201. *A. humistratus* Gray var. *humicavans* (Rydb.) Barn-
eby (ground cover milkvetch).
202. *A. kentrophyta* Gray (kentrophyta).
203. *A. lonchocarpus* Torr. (great rushy milkvetch).
204. *A. megacarpus* (Nutt.) Gray (bladdery milkvetch).
205. *A. miser* Dougl. ex Hook. (weedy milkvetch).
206. *A. tenellus* Pursh (Pursh milkvetch).
207. *Hedysarum boreale* Nutt. (northern sweetvetch).
208. *Lathyrus brachycalyx* Rydb. var. *zionis* (C. L.
Hitchc.) Welsh (sweetpea).
209. *Lotus utahensis* Ottley (Utah trefoil).
210. *Lupinus alpestris* A. Nels. (mountain lupine).
211. *L. argenteus* Pursh var. *tenellus* (Dougl.) Dunn (sil-
very lupine).
212. *L. kingii* S. Wats. var. *kingii* (King lupine).
213. *L. sericeus* Pursh var. *marianus* (Rydb.) Welsh
(silky lupine).
214. *Medicago lupulina* L. (black medic).
215. *M. sativa* L. (alfalfa).
216. *Melilotus officinalis* (L.) Lam. (yellow sweetclover).
217. *Oxytropis deflexa* (Pallas) DC var. *sericea* T & G
(locoweed).
218. *O. jonesii* Barneby (Jones oxytrope).
219. *O. oreophila* Gray var. *oreophila* (crazy weed).
220. *Psoralea pariensis* Welsh & Atwood (Paria bread-
root).
221. *Trifolium repens* L. (white clover).
222. *Vicia americana* Muhl. ex Willd. (American vetch).

Fagaceae

223. *Quercus gambelii* Nutt. (Gambel oak).

Gentianaceae

224. *Gentiana affinis* Criseb. (Rocky Mountain pleated
gentian).
225. *Gentiana amarella* L. var. *heterosepala* (Engelm.)
Gillett (gentian).
226. *G. dentonsa* Rottb. (fringed gentian).
227. *G. tenella* Rottb. (pygmy gentian).
228. *Swertia radiata* (Kellogg) Kuntze (elkweed; green
gentian).

Geraniaceae

229. *Geranium caespitosum* James (cranesbill).
230. *G. marginale* Rydb. (wild geranium).
231. *G. fremontii* Torr. (Fremont geranium).
232. *G. richardsonii* Fisch. & Trautv. (Richardson gera-
nium).

Iridaceae

233. *Iris missouriensis* Nutt. (Rocky Mountain iris).
234. *Sisyrinchium demissum* Greene (blue-eyed grass).

Juncaceae

235. *Juncus balticus* Willd. (wire rush).
236. *J. bufonius* L. (toad rush).
237. *J. ensifolius* Wikstr. (Rocky Mountain rush).
238. *J. longistylis* Torr. (rush).
239. *J. torreyi* Coville (Torrey rush).

Juncaginaceae

240. *Triglochin maritima* L. (greater arrowgrass).
241. *T. palustris* L. (lesser arrowgrass).

Lamiaceae (Labiatae)

242. *Hedeoma drummondii* Benth (mock pennyroyal).
243. *Marrubium vulgare* L. (horehound).
244. *Moldavica parviflora* (Nutt.) Britton (dragonhead).
245. *Monardella odoratissima* Benth. (monardella).
246. *Prunella vulgaris* L. (selfheal).

Liliaceae

247. *Allium acuminatum* Hook. (wild onion).
248. *A. nevadensis* S. Wats. (wild onion).
249. *Asparagus officinalis* L. (asparagus).
250. *Calochortus nuttallii* T & G (sego lily).
251. *Fritillaria atropurpurea* Nutt. (leopard lily).
252. *Leucocrinum montanum* Nutt. ex Gray (star lily).
253. *Smilacina stellata* (L.) Desf. (false Solomon's seal).
254. *Yucca angustissima* Engelm. ex Trelease (yucca).
255. *Y. harrimaniae* Trelease (yucca).
256. *Zigadenus elegans* Pursh (death camas).

Linaceae

257. *Linum aristatum* Engelm. (annual flax).
258. *L. kingii* S. Wats. (yellow flax).
259. *L. lewisii* Pursh (blue flax).

Loasaceae

260. *Mentzelia multiflora* (Nutt.) Gray (blazing star).

Loranthaceae

261. *Arceuthobium campylopodium* Engelm. (dwarf mis-
tletoe).
262. *A. douglasii* Engelm. (dwarf mistletoe).
263. *A. vaginatum* (Willd.) Presl. (dwarf mistletoe).
264. *Phoradendron juniperum* Engelm. (juniper mis-
tletoe).

Malvaceae

265. *Sphaeralcea coccinea* (Nutt.) Rydb. (globemallow).
266. *S. parvifolia* A. Nels. (globemallow).

Nyctaginaceae

267. *Abronia fragrans* Nutt. (snowball; sand verbena).
268. *A. nana* S. Wats. (tufted sand verbena).

Onagraceae

269. *Epilobium adenocaulon* Hausskn. (willow-weed).
270. *Gayophytum nuttallii* T & G (ground smoke).
271. *G. racemosum* T & G (ground smoke).
272. *Oenothera brachycarpa* Gray (giant evening prim-
rose).
273. *O. caespitosa* Nutt. (tufted evening primrose).
274. *O. coronopifolia* T & G (delicate evening primrose).
275. *O. flava* (A. Nels.) Garrett (yellow evening prim-
rose).
276. *O. lavandulaefolia* T & G (lavenderleaf evening
primrose).
277. *O. pallida* Lindl. (pale evening primrose).

Orchidaceae

278. *Corallorhiza maculata* Raf. (corallroot).
279. *C. striata* Lindl. (striped corallroot).
280. *Epipactis gigantea* Dougl. ex Hook. (giant hellebo-
rine).
281. *Habenaria sparsiflora* S. Wats. (bog orchid).

Orobanchaceae

282. *Orobancha fasciculata* Nutt. (broomrape).

Pinaceae

- 283. *Abies concolor* (Gord. & Glend.) Lindl. (white fir).
- 284. *Picea pungens* Engelm. (blue spruce).
- 285. *Pinus edulis* Engelm. (pinyon).
- 286. *P. flexilis* James (limber pine).
- 287. *P. longacta* D. K. Bailey (bristlecone pine).
- 288. *P. ponderosa* Laws. (ponderosa pine).
- 289. *Pseudotsuga menziesii* (Mirb) Franco (Douglas-fir).

Plantaginaceae

- 290. *Plantago eriopoda* Torr. (redwood plantain).
- 291. *P. lanceolata* L. (lanceleaf plantain).

Poaceae (Gramineae)

- 292. *Agropyron cristatum* (L.) Gaertn. (crested wheatgrass).
- 293. *A. dasystachyum* (Hook.) Scribn. var. *dasystachyum* (thickspike wheatgrass).
- 294. *A. scribneri* Vasey (Scribner wheatgrass).
- 295. *A. smithii* Rydb. (Western wheatgrass).
- 296. *A. spicatum* (Pursh) Scribner & Smith var. *inermis* (Scribn. & Smith) Heller (bluebunch wheatgrass).
- 297. *A. trachycaulum* (Link) Malte var. *trachycaulum* (slender wheatgrass).
- 298. *A. trachycaulum* (Link) Malte var. *unilaterale* (Cassidy) Malte (bearded wheatgrass).
- 299. *Agrostis stolonifera* L. (redtop; bentgrass).
- 300. *Aristida fendleriana* Steud. (three-awn).
- 301. *Arundo donax* L. (giant reed).
- 302. *Bouteloua gracilis* (HBK) Lag. ex Steud. (blue grama).
- 303. *Bromus anomalous* Rupr. ex Fourn (nodding brome).
- 304. *B. carinatus* Hook. & Arn (California brome).
- 305. *B. ciliatus* L. (fringed brome).
- 306. *B. commutatus* Schrader (hairy chess).
- 307. *B. inermis* Leysser (smooth brome).
- 308. *B. tectorum* L. (cheatgrass).
- 309. *Calamagrostis neglecta* (Ehrh.) Gaertn., Meyer & Schreb. (subalpine reedgrass).
- 310. *C. scopulorum* M. E. Jones (reedgrass).
- 311. *Dactylis glomerata* L. (orchard grass).
- 312. *Deschampsia cespitosa* (L.) Beauv. (hairgrass).
- 313. *Elymus junceus* Fischer (Russian wildrye).
- 314. *E. canadensis* L. (Canada wildrye).
- 315. *E. salina* M. E. Jones (salina wildrye).
- 316. *Festuca ovina* L. var. *rydbergii* St.-Yves (sheep fescue).
- 317. *F. pratensis* Hud. (meadow fescue).
- 318. *Glyceria striata* (Lam.) A. S. Hitchc. (fowl manna-grass).
- 319. *Hilaria jamesii* (Torr.) Benth. (galleta).
- 320. *Hordeum brachyantherum* Nevski (meadow barley).
- 321. *H. jubatum* L. (foxtail barley).
- 322. *Koeleria nitida* Nutt. (junegrass).
- 323. *Muhlenbergia andina* (Nutt.) A. S. Hitchc. (foxtail muhly).
- 324. *M. asperifolia* (Nees & Meyer) L. R. Parodi (scratchgrass).
- 325. *M. montana* (Nutt.) A. S. Hitchc. (mountain muhly).
- 326. *M. pungens* Thurber (sandhill muhly).
- 327. *M. richardsonis* (Trin.) Rydb. (mat muhly).
- 328. *Oryzopsis hymenoides* (Roemer & Schultes) Ricker (Indian ricegrass).
- 329. *O. micrantha* (Trin. & Rupr.) Thurber (little ricegrass).

- 330. *Phleum pratense* L. (timothy).
- 331. *Poa compressa* L. (Canada bluegrass).
- 332. *P. fendleriana* (Steud.) Vasey (mutton grass).
- 333. *P. nevadensis* Vasey ex Scribn. (Nevada bluegrass).
- 334. *P. pratensis* L. (Kentucky bluegrass).
- 335. *P. reflexa* Vasey & Scribn. (nodding bluegrass).
- 336. *Sitanion hystrix* (Nutt.) J. G. Smith (squirreltail).
- 337. *Sporobolus airoides* (Torr.) Torr. (alkali sacaton).
- 338. *Stipa columbiana* Macoun (Columbia needlegrass).
- 339. *S. comata* Trin. & Rupr. (needle-and-thread grass).
- 340. *S. lettermanii* Vasey (letterman needlegrass).
- 341. *X. Stiporyzopsis bloomeri* (Boland) B. L. Johnson (fool's ricegrass).

Polemoniaceae

- 342. *Ipomopsis aggregata* (Pursh) Spreng. (skyrocket gilia).
- 343. *Gilia congesta* Hook. var. *congesta* (ballhead gilia).
- 344. *Leptodactylon pungens* (Torr.) Nutt. (prickly phlox).
- 345. *Linanthastrum nuttallii* (Gray) Ewan (false phlox).
- 346. *Phlox austromontana* Cov. (mountain phlox).
- 347. *P. condensata* (Gray) E. Nels. (creeping phlox).
- 348. *P. diffusa* Benth (spreading phlox).
- 349. *P. longifolia* Nutt. (longleaf phlox).
- 350. *P. muscoides* Nutt. (mossy phlox).
- 351. *Polemonium occidentale* Greene (Jacob's ladder).
- 352. *P. viscosum* Nutt. (Jacob's ladder).

Polygonaceae

- 353. *Eriogonum alatum* Torr. var. *alatum* (winged buckwheat).
- 354. *E. corymbosum* Benth. in DC var. *corymbosum* (shrubby buckwheat).
- 355. *E. microthecum* Nutt. var. *foliosum* (T & G) Reveal (slimleaf buckwheat).
- 356. *E. panguicense* (M. E. Jones) Reveal var. *panguicense* (Panguitch buckwheat).
- 357. *E. racemosum* Nutt. (redroot buckwheat).
- 358. *E. subreniforme* S. Wats. (kidney-leaf buckwheat).
- 359. *E. umbellatum* Torr. var. *subaridum* Stokes (sul-furflowered buckwheat).
- 360. *Polygonum aviculare* L. (creeping jenny).
- 361. *P. douglasii* Greene var. *johnstonii* Munz (sawatch knotweed).
- 362. *P. ramosissimum* Michx. (bush knotweed).
- 363. *P. viviparum* L. (viviparous knotweed).
- 364. *Rumex crispus* L. (curly dock).
- 365. *R. triangulivalis* (Danser) Rech. (dock).

Polypodiaceae

- 366. *Cheilanthes feei* T. Moore (lipfern).
- 367. *Pteridium aquilinum* (L.) Kuhn (bracken fern).

Primulaceae

- 368. *Androsace septentrionalis* L. (rock jasmine).
- 369. *Dodecatheon pulchellum* (Raf.) Merrill (shooting star).

Pyrolaceae

- 370. *Pyrola asarifolia* Michx. (alpine pyrola).
- 371. *P. cirens* Schweigg (pyrola).
- 372. *Pteropora andromeda* Nutt. (pinedrops).

Ranunculaceae

- 373. *Aconitum columbianum* Nutt. (monkshood).
- 374. *Anemone multifida* Poir. (anemone).
- 375. *Aquilegia caerulea* James (Colorado columbine).

376. *A. scopulorum* Tides. (rock columbine).
377. *Clematis ligusticifolia* Nutt. (western virgin's bow-er).
378. *C. pseudoalpina* (Kuntze) A. Nels. (Rocky Mountain clematis).
379. *Delphinium scaposum* Greene (larkspur).
380. *Ranunculus cymbalaria* Pursh (Rocky Mountain buttercup).
381. *R. flammula* L. (creeping buttercup).
382. *R. inamoenus* Greene (buttercup).
383. *Thalictrum fendleri* Engelm. (meadow rue).

Rhamnaceae

384. *Ceanothus fendleri* Gray (Fendler buckbrush).
385. *C. martinii* M. E. Jones (Martin buckbrush).

Rosaceae

386. *Amelanchier utahensis* Koehne (serviceberry).
387. *Cercocarpus ledifolius* Nutt. (curlleaf mountain mahogany).
388. *C. montanus* Raf. (birch-leaf mountain mahogany).
389. *Cowania mexicana* D. Don (cliffrose).
390. *Fallugia paradoxa* (D. Don) Endl. (apache plume).
391. *Fragaria vesca* L. var. *bracteata* (Heller) R. J. Davis (wild strawberry).
392. *Holodiscus dumosus* (Hook.) Heller (ocean spray; rock spirea).
393. *Ivesia sabulosa* (M. E. Jones) Keck (ivesia).
394. *Paraphyllum ramosissimum* Nutt. (squawapple).
395. *Potentilla anserina* L. (silverweed cinquefoil).
396. *P. concinna* Richards (elegant cinquefoil).
397. *P. crinita* Gray (cinquefoil).
398. *P. fruticosa* L. (shrubby cinquefoil).
399. *P. gracilis* Dougl. var. *pulcherrima* (Lehm.) Fern. (common cinquefoil).
400. *P. plattensis* Nutt. (Platte cinquefoil).
401. *Prunus virginiana* L. (choke cherry).
402. *Purshia tridentata* (Pursh) DC (bitterbrush).
403. *Rosa nutkana* Presl. (Nutka rose).
404. *R. woodsii* Lindl. (wild rose).
405. *Rubus idaeus* L. var. *sachalinensis* (Levl.) Focke (wild raspberry).

Rubiaceae

406. *Galium trifidum* L. (bedstraw).
407. *Kelloggia galioides* Torr. (pseudobedstraw).

Salicaceae

408. *Populus angustifolia* James (narrowleaf cottonwood).
409. *P. fremontii* S. Wats. (Fremont cottonwood).
410. *P. tremuloides* Michx. (quaking aspen).
411. *Salix bebbiana* Sarg. (Bebb willow).
412. *S. drummondiana* Barratt (Drummond willow).
413. *S. exigua* Nutt. (sandbar willow).
414. *S. geyeriana* Anderss. (Geyer willow).
415. *S. lasiandra* Benth. var. *caudata* (Nutt.) Sudw. (Pacific willow).

Santalaceae

416. *Comandra pallida* A. DC (bastard toadflax).

Saxifragaceae

417. *Lithophragma tenella* Nutt. (woodland star).
418. *Parnassia parviflora* DC (grass-of-Parnassus).
419. *Ribes aureum* Pursh (gooseberry).
420. *R. cereum* Dougl. (wax currant).

Scrophulariaceae

421. *Castilleja chromosa* A. Nels. (Indian paintbrush).
422. *C. linariaefolia* Benth. (Wyoming paintbrush).
423. *C. revealii* N. Holmgren (Reveal paintbrush).
424. *Cordylanthus kingii* S. Wats. (birdbeak).
425. *Mimulus guttatus* DC (monkey flower).
426. *M. rubellus* Gray (annual monkey flower).
427. *Orthocarpus luteus* Nutt. (yellow owllover).
428. *O. purpureo-albus* Gray (purple-white owllover).
429. *Pedicularis centranthera* Gray (lousewort).
430. *Penstemon bracteatus* Keck (Red Canyon beard-tongue).
431. *P. bridgesii* Gray (redfish).
432. *P. caespitosus* Nutt. (mat penstemon).
433. *P. comarrhenus* Gray (dusty penstemon).
434. *P. eatonii* Gray (Eaton penstemon).
435. *P. leiophyllus* Pennell (royal blue penstemon).
436. *P. rydbergii* A. Nels. (Rydberg penstemon).
437. *P. utahensis* Eastw. (Utah penstemon).
438. *Verbascum thapsus* L. (flannel mullein).
439. *Veronica americana* Schw. (American speedwell).

Solanaceae

440. *Solanum triflorum* Nutt. (cutleaf nightshade).

Tamaricaceae

441. *Tamarix pentandra* Pall. (tamarisk).

Valerianaceae

442. *Valeriana acutiloba* Rydb. (valerian).
443. *V. edulis* Nutt. (edible valerian).

Verbenaceae

444. *Verbena bracteata* Lag. & Rodr. (vervain).

Violaceae

445. *Viola adunca* J. E. Smith (blue violet).
446. *V. purpurea* Kellogg (goosefoot violet).

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NOMENCLATURAL CHANGES AND NEW SPECIES IN PLATYPODIDAE AND SCOLYTIDAE (COLEOPTERA)

Stephen L. Wood¹

ABSTRACT.— New names are presented to replace junior homonyms as follows in Platypodidae: *Platypus acuticornifer* for *Platypus acuticornis* Schedl, 1975 (nec Schedl, 1973), *Platypus tuberculifer* for *Platypus bituberculatus* Schedl, 1975 (nec Nunberg, 1967), *Platypus obliquus* for *Platypus obliquesectus* Schedl, 1975 (nec Schedl, 1973); and in Scolytidae: *Amphicranus electus* for *Amphicranus elegantulus* Schedl, 1978 (nec Schedl, 1963), *Araptus crassulus* for *Araptus crassus* Wood (nec Schedl, 1966), *Corthycyclon tardulus* for *Corthycyclon tardus* Schedl, 1976 (nec Wood, 1974), *Corthylus brunnescens* for *Corthylus brunneus* Wood, December 1974 (nec Schedl, November 1974), *Monarthrum denticulatum* for *Monarthrum* (= *Pterocyclon*) *dentatum* Eggers, 1941 (nec Eggers, 1935), *Monarthrum peruvianum* for *Monarthrum peruanum* Schedl, 1978 (nec Schedl, 1950), *Scolytodes eximius* for *Scolytodes grandis* Schedl, 1978 (nec Schedl, 1962), *Scolytodes minutus* for *Scolytodes* (= *Hexacolus*) *minutissimus* Schedl, 1978 (nec Schedl, 1952). New synonymy is proposed in Platypodidae for *Genyocerus albipennis* Motschulsky (= *Diacavus irregularis* Browne). The emendation in Scolytidae of *Cnemonyx vismiacolens* is presented to correct the lapsus calami *Cnemonyx vismiacolens* Wood, 1979. The following species of Scolytidae are named as new to science: *Chramesus atkinsoni*, *Liparthrum thevetiae*, *Microborus mexicanus*, *Phloeocleptus ardis*, *Phloeocleptus atkinsoni*, *Phloeocleptus cristatus*, *Phloeocleptus spicatus*, *Pseudothyasanoes perseae* (Mexico), *Scolytodes anceps*, *Scolytodes pusillimus*, *Scolytodes tardus*, *Scolytodes resculus* (Colombia), *Scolytodes ficolens*, *Scolytodes naevius* (Venezuela).

While updating my taxonomic files of bark and ambrosia beetles, I found several homonyms that require new names and a few other taxonomic and nomenclatural errors that require correction. These are summarized in the above abstract. In addition, 14 species of Scolytidae are described as new to science. These are presented in alphabetical order and represent the genera *Chramesus* (1), *Liparthrum* (1), *Microborus* (1), *Phloeocleptus* (4), *Pseudothyasanoes* (1), and *Scolytodes* (6) and are from the following countries: Mexico (8), Colombia (4), and Venezuela (2).

NEW NAMES IN PLATYPODIDAE

Platypus acuticornifer, n. n.

Platypus acuticornis Schedl, 1975, Reichenbachia 15:223 (Holotype, male; Luth. Miss. Sawmill, Porotop, Papua; Schedl Coll.). *Preoccupied*

The name *Platypus acuticornis* Schedl, 1975, is preoccupied by Schedl, 1973 (Papua New Guinea Agric. J. 24:77), and must be replaced. The new name *acuticornifer* is proposed as a replacement.

Platypus bituberculifer, n. n.

Platypus bituberculatus Schedl, 1975, Reichenbachia 15:224 (Holotype, male; Wau, Morobe Distr., New Guinea; Schedl Coll.). *Preoccupied*

The name *Platypus bituberculatus* Schedl, 1975, is preoccupied by Nunberg, 1967 (Rev. Zool. Bot. Afr. 76:325), and must be replaced. The new name *bituberculifer* is proposed as a replacement.

Platypus obliquus, n. n.

Platypus obliquesectus Schedl, 1975, Reichenbachia 15:229 (Holotype, male; Mt. Wilhelm, New Guinea; Schedl Coll.). *Preoccupied*

The name *Platypus obliquesectus* Schedl, 1975, is preoccupied by Schedl, 1973 (Papua New Guinea Agric. J. 24:77), and must be replaced. The new name *obliquus* is proposed as a replacement.

NEW SYNONYMY IN PLATYPODIDAE

Genyocerus albipennis Motschulsky

Genyocerus albipennis Motschulsky, 1858, Etudes Entomologiques 7:68 (Holotype, female; Ceylon; Zool.

¹Life Science Museum and Department of Zoology, Brigham Young University, Provo, Utah 84602. Scolytidae contribution No. 71.

Instit. USSR, Moscow); Wood, 1969, Great Basin Nat. 29:118 (holotype redescribed)

Diacavus irregularis Browne, 1970, J. Nat. Hist. 4:582 (Holotype, male; intercepted in timber from Ceylon at Princes Risborough, England; British Mus. Nat. Hist.). *New synonymy*

Notes and sketches based on the holotype of *Genyocerus albipennis* Motschulsky were made by me in 1968 then used in 1975 to identify a common representative of this genus from Ceylon. Part of the 1975 series was compared in 1977 by F. G. Browne to the holotype of *Diacavus irregularis* Browne and found to be identical. Since the species is common at its type locality and easily recognized from an abundance of characters, it is concluded that Browne's name must be placed in synonymy as indicated above.

NEW NAMES IN SCOLYTIDAE

Amphicranus electus, n. n.

Amphicranus elegantulus Schedl, 1978, Ent. Abh. Mus. Tierk. Dresden 41:304 (Holotype, sex?; Alt. Ampara, Brazil; Schedl Coll.). *Preoccupied*

The name *Amphicranus elegantulus* Schedl, 1978, is preoccupied by Schedl, 1963 (*Reichenbachia* 1:225), and must be replaced. The new name *electus* is proposed as a replacement.

Araptus crassulus, n. n.

Araptus crassus Wood, 1977, Great Basin Nat. 37:211 (Holotype, female ?; 8 km NE Cerro Jefe, Panama; Wood Coll.). *Preoccupied*

The name *Araptus crassus* Wood, 1977, is preoccupied by Schedl, 1966 (validated as *Thamnophthorus crassus*, Ent. Arb. Mus. Frey 17:108). Because *Araptus* and *Thamnophthorus* are synonymous, the junior name must be replaced. The new name *crassulus* is proposed as a replacement.

Corthycyclon tardulus, n. n.

Corthycyclon tardus Schedl, 1976, Ent. Abh. Mus. Tierk. Dresden 41:85 (Holotype, male?; Pernambuco, Caruaru, Brazil; Schedl Coll.). *Preoccupied*

The name *Corthycyclon tardus* Schedl, 1976, is preoccupied by Wood, 1974 (Great Basin Nat. 34:149), and must be replaced. The new name *tardulus* is proposed as a replacement.

Corthylus brunnescens, n. n.

Corthylus brunneus Wood, 1974, Great Basin Nat. 34:188 (Holotype, female; Volcan Barba, Heredia, Costa Rica; Wood Coll.). *Preoccupied*

The name *Corthylus brunneus* Wood, 1974, is preoccupied by Nunberg, 1972 (Pap. Avuls. Zool., S. Paulo 25:191), and must be replaced. The new name *brunnescens* is proposed as a replacement.

Monarthrum denticulatum, n. n.

Pterocyclon dentatum Eggers, 1941, Arb. Morph. Taxon. Ent. Berlin-Dahlem 8:101 (Holotype, male; Trois Rivières, Guadeloupe; Eggers Coll., apparently on loan to Schedl). *Preoccupied*

The genera *Monarthrum* and *Pterocyclon* were placed in synonymy by Wood (1966, Great Basin Nat. 26:19). When *P. dentatum* Eggers, 1941, was transferred to *Monarthrum*, the name was preoccupied by Eggers, 1935 (Rev. de Ent. 5:84), and must be replaced. The new name *denticulatum* is proposed as a replacement.

Monarthrum peruvianum, n. n.

Monarthrum peruanum Schedl, 1978, Ent. Abh. Mus. Tierk. Dresden 41:306 (Holotype, female; Enseñas, Tambo, Peru; Schedl Coll.). *Preoccupied*

The name *Monarthrum peruanum* Schedl, 1978, is preoccupied by Schedl, 1950 (validated as *Pterocyclon peruanum*, *Dusenja* 1:168). Since *Monarthrum* and *Pterocyclon* are synonymous, the junior name must be replaced. The new name *peruvianum* is proposed as a replacement.

Scolytodes eximius, n. n.

Scolytodes grandis Schedl, 1978, Ent. Abh. Mus. Tierk. Dresden 41:298 (Holotype, sex?; Machu-Picchu, Peru; Schedl Coll.). *Preoccupied*

The name *Scolytodes grandis* Schedl, 1978, is preoccupied by Schedl, 1962 (validated as *Hexacolus grandis*, Mitt. Münchn. Ent. Ges. 52:100). Since *Scolytodes* and *Hexacolus* are synonymous, the junior name must be replaced. The new name *eximius* is proposed as a replacement.

Scolytodes minutus, n. n.

Hexacolus minutissimus Schedl, 1978, Ent. Abh. Mus. Tierk. Dresden 41:297 (Holotype, sex?; Nova Teutonia, Brazil; Schedl Coll.). *Preoccupied*

The genera *Scolytodes* and *Hexacolus* were placed in synonymy by Wood (1971), Great Basin Nat. 31:141. When *H. minutissimus* Schedl, 1978, was transferred to *Scolytodes* the name was preoccupied by Schedl, 1952 (*Dusenja* 3:355); consequently, the junior name must be replaced. The new name *minutus* is proposed as a replacement.

AN EMENDATION IN SCOLYTIDAE

Cnemonyx vismiacolens Wood, emendation

Cnemonyx vismiacolens Wood, 1979, Great Basin Nat. 39:138 (Holotype, female; Merida, Merida, Venezuela; Wood Coll.)

This species was named for its host association with *Vismia* sp. In the original publication, the name was inadvertently spelled *vismiacolens* (a lapsis calami) and should be corrected to *vismiacolens* to conform to the spelling of the host genus.

NEW TAXA

Chramesus atkinsoni, n. sp.

This species is distinguished from *hickoriae* LeConte by the different elytral vestiture as described below and by other minor characters.

MALE.—Length 1.7 mm (paratypes 1.6–1.8 mm), 1.5 times as long as wide; color very dark brown.

Frons similar to *hickoriae* except excavated area very slightly wider in proportion to its length (length/width = 1.36 compared to 1.42).

Pronotum similar to *hickoriae* except more strongly convex (females do not differ in this character).

Elytra similar to *hickoriae* except interstitial setae in ground cover (forming rows at each interstitial margin) more slender, erect bristles stouter and much shorter, bristles spaced between rows by one and one-third times length of a bristle, by length of a bristle within a row (bristles slightly longer than either distance in *hickoriae*); each bristle about eight times as long as wide.

FEMALE.—Similar to male except frons convex and unarmed by a pair of tubercles; pronotum more strongly convex and with asperities averaging larger.

TYPE LOCALITY.—Cerro Chipinque, Monterrey, Nuevo León, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and two male paratypes were taken at the type locality on 31-V-1980, 1350 m, No. S-021, from *Persea*, by T. H. Atkinson.

The holotype, allotype, and paratypes are in my collection.

Liparthrum thevetiae, n. sp.

This species is distinguished from *albosetosum* (Bright) by the smaller size, by the smaller, less strongly impressed stria punctures on the disc, and by the more slender interstitial scales.

FEMALE.—Length 0.8 mm (paratypes 0.8–0.9 mm), 2.2 times as long as wide; color very dark brown, vestiture pale.

Frons largely concealed in specimens at hand, convex, apparently about as in *albosetosum*.

Pronotum about as in *albosetosum* except asperities slightly larger, scales less abundant, shorter, and wider.

Elytra about as in *albosetosum* except only three or four basal crenulations present, first three contiguous (five in *albosetosum*); stria punctures smaller, less strongly impressed; interstitial scales smaller, little if any longer than wide, spaced within a row by three to five lengths of a scale and alternating within a row with slender setae each about one and one-half times as long as a scale, scales about two-thirds as long as distance between rows.

TYPE LOCALITY.—Las Piedras Moyotepec, Morelos, Mexico.

TYPE MATERIAL.—The female holotype and four female paratypes were taken at the type locality on 17-VII-1980, 1060 m, from *Thevetia ovata*, by T. H. Atkinson.

The holotype and paratypes are in my collection.

Microborus mexicanus, n. sp.

This species is the most aberrant in the genus. It is distinguished from *lautus* Wood by the darker color, by the stouter body and pronotum, by the different declivity, and by other characters described below.

MALE.—Length 1.1 mm (paratypes 1.0–1.1 mm), 2.3 times as long as wide; color very dark brown to almost black.

Frons convex, reticulate; eyes separated above by 2.5 times width of an eye. Antenna typical of genus, with funicle stouter than normal.

Pronotum 1.1 times as long as wide; sides straight and parallel on basal half, rather broadly rounded in front; surface smooth, shining, punctures rather coarse, deep, spaced by less than diameter of a puncture. Short hairlike setae arise from punctures, each about as long as diameter of a puncture.

Elytra 1.3 times as long as wide, 1.4 times as long as pronotum; outline and disc as in *lautus* except striae more distinctly impressed; declivity steeper than but similar to *lautus* except on declivity; interstriae 7 and 9 more acutely carinate, acute carina continuing from their junction to apex; striae continue to base, only very slightly shorter than those of interstriae; interstitial setae extend to base, close, uniseriate on disc, each three-fourths as long as distance between rows, slightly longer on declivity, slightly confused on 2 and 3.

FEMALE.—Similar to male except setae on declivital interstriae 2 and 3 less distinctly confused.

TYPE LOCALITY.—Las Piedras, Moyotepec, Morelos, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and three paratypes were taken at the type locality on 17-VII-1980, 1060 m, No. S-077, from *Bursera*, by T. H. Atkinson.

The holotype, allotype, and paratypes are in my collection.

Phloeocleptus ardis, n. sp.

This species is distinguished from *spicatus* Wood, described below, by the larger size, by the slightly flattened, smoother, more finely punctured frons, by the less abrupt, more evenly convex male declivity, and by the smaller circumdeclivital male spines.

MALE.—Length 1.7 mm (paratypes 1.7–1.9 mm), 2.5 times as long as wide; almost black except pronotal summit reddish brown.

Frons as in *spicatus* except central third almost subconcavely impressed, smooth, shining, with a few obscure, minute punctures. Scape broad, with a large tuft of long yellow hair.

Pronotum as in *spicatus*.

Elytra about as in *spicatus* except discal punctures slightly smaller, base of declivity less abrupt, spines in circumdeclivital ring distinctly smaller, much less sharply pointed, declivital punctures slightly smaller, vestiture finer.

TYPE LOCALITY.—Cerro Chipinque, Monterrey, Nuevo León, Mexico.

TYPE MATERIAL.—The male holotype and four male paratypes were taken at the type locality on 30-I-1980, 1300 m, No. S-020, from *Persea*, by T. H. Atkinson.

The holotype and paratypes are in my collection.

Phloeocleptus atkinsoni, n. sp.

This species is distinguished from *obscurus* Wood by the elevated crest of declivital interstriae 9 continuing almost to the suture, by the presence of tubercles on declivital interstriae 2, and by the presence of four serrations on the anterior margin of the pronotum.

MALE.—Length 1.2 mm (paratypes 1.1–1.2 mm), 2.7 times as long as wide; color almost black, except summit of pronotum almost reddish brown.

Frons broadly convex; surface apparently finely granulate-punctate.

Pronotum similar to *obscurus* except constriction on anterior half more pronounced and posterior areas conspicuously reticulate-granulate; anterior margin armed by four equal, subcontiguous serrations.

Elytra similar to *obscurus* except striae punctures on disc conspicuously larger, deeper, interstitial granules larger, moderately elevated, crest of interstriae 9 continuing at least to striae 2, declivital interstriae 2 armed by granules and bearing setae similar to those on 1 and 3, vestiture more slender and longer.

FEMALE.—Similar to male except antennal scape more strongly expanded and ornamented by a larger tuft of hair, anterior margin of pronotum unarmed by serrations, and declivital interstriae 9 less strongly elevated.

TYPE LOCALITY.—Uruapan, Michoacán, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and three female paratypes were taken at the type locality on 17-II-1980, No. S-026, 1600 m, from *Persea*, by T. H. Atkinson.

The holotype, allotype, and paratypes are in my collection.

Phloeocleptus cristatus, n. sp.

This species is distinguished from *obscurus* Wood by the larger size and by the very different elytral declivity as described below.

MALE.—Length 1.4 mm (paratypes 1.2–1.4 mm), 2.4 times as long as wide; color almost black except summit of pronotum almost reddish brown.

Frons and pronotum about as in *obscurus* except anterior margin of pronotum armed by four rather widely spaced serrations, lateral pair submarginal.

Elytral disc about as in *obscurus* except most interstitial punctures obscurely or incompletely replaced by granules; declivity more broadly convex, somewhat impressed in ventrolateral areas, interstriae 9 strongly, acutely elevated, anterior and posterior limits of this elevation rather abrupt, elevation ending posteriorly at striae 3 but with tubercles on interstriae 1 and 2 suggesting a continuation of it, interstriae 2 with a row of fine tubercles and setae on upper half, vestiture more slender.

FEMALE.—Similar to male except antennal scape slightly larger and with a larger tuft of setae, anterior margin of pronotum unarmed, declivital interstriae 9 less strongly elevated, more conspicuously serrate.

TYPE LOCALITY.—Tepoztlan, Morelos, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and three paratypes were taken at the type locality on 20-VI-1980, No. S-071, from *Persea*, by T. H. Atkinson.

The holotype, allotype, and paratypes are in my collection.

Phloeocleptus spicatus, n. sp.

This species is distinguished from *caudatus* Wood by the smaller size, by the antennal scape being wider than long in both sexes, by the absence of tubercles on declivital striae 2 in both sexes, and by the very different male declivity.

MALE.—Length 1.25 mm (paratypes 1.0–1.2 mm), 2.4 times as long as wide; color almost black except summit of pronotum almost reddish brown.

Frons broadly convex, finely, unevenly rugose. Antennal scape as wide as long, ornamented by a small tuft of hair.

Pronotum about as in *caudatus* except serrations on anterior margin poorly, irregularly formed.

Elytra with sides almost straight and parallel on basal three-fourths, abruptly subtruncate at declivity, submucronate behind; striae weakly impressed on posterior half of disc, punctures sharply, deeply impressed, increasing in size posteriorly; interstriae slightly wider than striae at base, slightly narrower at base of declivity, punctures small, obscure, apparently uniseriate, granulate near declivity except on 1 and 2 extending to middle of disc. Declivity moderately abrupt, steep, convex; basal margin with a circumdeclivital ring of moderately large, sharply pointed spines on 2 to 8, spine on 3 positioned slightly behind others, subserrate on 9 to apex; striae punctures continuing to declivity, coarse deep; interstriae 1 and 3 weakly elevated, each with a row of fine denticles on basal half. Vestiture of rows of short striae and longer interstitial hair.

FEMALE.—Similar to male except scape much more strongly widened and with a larger tuft of hair; anterior margin of pronotum unarmed; striae punctures small, not enlarged posteriorly; declivity more gradually, evenly convex, without a circumdeclivital row of spines, interstriae 9 only slightly elevated.

TYPE LOCALITY.—Cerro Chipinque, Monterrey, Nuevo León, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and two female paratypes were taken at the type locality on 30-I-80, 1300 m, No. S-020, from *Persea*, by T. H. Atkinson.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes perseae, n. sp.

This species is distinguished from *dislocatus* (Blackman) by the more slender body, by the more distinct striae punctures on the disc, by the longer, more slender elytral scales, and by other characters described below.

MALE.—Length 1.0 mm (female paratypes 1.2 mm), 2.4 (female 2.7) times as long as wide; color brown.

Frons more broadly, evenly convex than in *dislocatus*, fovea similar. Antenna as in *dislocatus*.

Pronotum as in *dislocatus* except more slender and scales stouter.

Elytra more slender than in *dislocatus*, discal punctures more clearly impressed, declivity steeper, declivital punctures not deeper but more clearly formed, interstitial scales distinctly longer, each six to eight times as long as wide.

FEMALE.— Similar to male except much more slender; frons moderately, concavely impressed to upper level of eyes (stronger and more extensive than in *dislocatus*) and foveate at center, without setal ornamentation; scape with a tuft of long hair; anterior margin of pronotum unarmed; interstitial setae more slender, each at least eight times as long as wide.

TYPE LOCALITY.— Cerro Chipinque, Monterrey, Nuevo León, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and three paratypes were taken at the type locality on 31-I-1980, 1350 m, No. S-021, from *Persea*, by T. H. Atkinson.

The holotype, allotype, and paratypes are in my collection.

Scolytodes anceps, n. sp.

This species is distinguished from *irazuensis* Wood by the smaller size, by the much smaller pronotal and elytral punctures, and by the different sculpture and setal ornamentation of the female frons as described below.

FEMALE.— Length 1.3 mm (paratypes 1.3–1.5 mm), 2.4 times as long as wide; color very dark brown.

Frons about as in *irazuensis* except epistomal area reticulate, middle third more coarsely punctured, area above eyes not flattened, vestiture finer, much less abundant on lower third.

Pronotum about as in *irazuensis* except anterior areas entirely devoid of indications of asperities, punctures minute, many almost obsolete.

Elytra similar to *irazuensis* except striae punctures minute, almost obsolete, interstitial punctures mostly obsolete; odd-numbered interstriae each with about four to six widely spaced, slender setae scattered between base and apex.

MALE.— Similar to female except frons evenly convex, surface uniformly reticulate, without carinae or ornamental setae.

TYPE LOCALITY.— Piedras Blancas, 11 km W Medellin, Antioquia, Colombia.

TYPE MATERIAL.— The female holotype, male allotype, and 58 paratypes were taken at the type locality on 17-VII-1970, 2300 m, No. 691, from *Cecropia* petioles, by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes ficicolens, n. sp.

This species is distinguished from *irazuensis* Wood by the slightly larger size, by the slight differences in the female frons as described below, by the larger, more numerous pronotal asperities, by the smaller striae and larger interstitial punctures, and by other characters.

FEMALE.— Length 1.8 mm (paratypes 1.7–1.9 mm), 2.5 times as long as wide; color very dark brown.

Frons similar to *irazuensis* except carinae more acutely elevated, slightly arcuate, more widely separated, median area more broadly flattened, more finely punctured, vestiture similar but slightly longer and more abundant, particularly in central area.

Pronotum similar to *irazuensis* except entire surface strongly reticulate, punctures on posterior half slightly larger, anterior third with numerous, fine asperities, these decreasing in height posteriorly to become little more than smooth shining spots on anterior margins of punctures on basal half. Vestiture of sparse setae in marginal areas.

Elytra 1.6 times as long as wide; about as in *irazuensis* except striae not impressed, punctures smaller, not as deep, in rows, indistinguishable from those of interstriae, both striae and interstitial punctures bear minute setae (each little longer than diameter of a puncture), some interstitial punctures on odd-interstriae bearing erect, moderately long setae, these sparse on disc, somewhat closer on declivity.

MALE.— Similar to female except frons convex, surface rugose-reticulate, without carinae or ornamental setae.

TYPE LOCALITY.— Merida, Merida, Venezuela.

TYPE MATERIAL.— The female holotype, male allotype, and 22 paratypes were taken

at the type locality on 7-X-1969, 170 m, No. 42, from *Ficus* branches by me; 16 additional paratypes bear the same data except they were taken 22-IX-1969, No. 8.

The holotype, allotype, and paratypes are in my collection.

Scolytodes naevius, n. sp.

This species is distinguished from *subparallelus* (Eggers) by the rather strongly reticulate pronotum, and by the presence of very minute, moderately abundant striae and interstitial setae on the declivity (entirely glabrous in *subparallelus*).

FEMALE.—Length 1.5 mm (paratypes 1.3–1.6 mm), 2.3 times as long as wide; color yellowish brown.

Frons moderately concave except plano-concave on median third of lower half, a pair of weak, shining calluses at dorsolateral margins of impressed area; finely, rather closely punctured in central area except almost impunctate on calluses, more densely punctured on upper and lateral margins of impressed area; vestiture of fine, long, yellow hair on lateral and upper margins up to (below) three-fourths of distance from epistoma to upper level of eyes.

Pronotum 1.0 times as long as wide; sides almost straight and parallel on middle half, rather broadly rounded in front; anterior margin finely serrate; anterior half rather coarsely, closely asperate, punctures not evident; posterior half strongly reticulate, punctures fine, obscure. Glabrous except for sparse setae near margins.

Elytra 1.5 times as long as wide, 1.6 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, punctures very small, very shallow; interstriae four or more times as wide as striae, smooth, shining, punctures very small, uniseriate, rather close. Declivity convex, steep; sculpture about as on disc. Vestiture consisting of minute striae and interstitial setae, each only slightly longer than diameter of very small puncture.

MALE.—Similar to female except frons convex, reticulate, without calluses or ornamental setae; serrations on anterior margin of pronotum distinctly larger.

TYPE LOCALITY.—Forty km SE Socopo, Barinas, Venezuela.

TYPE MATERIAL.—The female holotype, male allotype, and 29 paratypes were taken at the type locality on 25-I-1970, 150 m, No. 277, from *Clusia*, by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes pusillimus, n. sp.

This species is distinguished from *impressus* Wood by the smaller size, by the less strongly impressed striae 2–6, and by the longer, much more slender interstitial setae.

FEMALE.—Length 1.2 mm (paratypes 1.0–1.2 mm), 2.6 times as long as wide; color dark reddish brown.

Frons as in *impressus* except obscure reticulation on upper half (mostly on lower half in *impressus*), without special setal ornamentation in either species.

Pronotum as in *impressus*.

Elytra as in *impressus* except interstriae 1 on disc and declivity rather strongly impressed, others not impressed, striae punctures slightly smaller, interstitial setae slender, almost hairlike, slightly longer, each seta equal in length to distance between rows and between setae within a row.

MALE.—Similar to female except costa on anterior margin of pronotum more strongly elevated, interstitial setae stouter, blunt at their apices and most very slightly flattened on their apical thirds.

TYPE LOCALITY.—Twenty-seven km north-east of Montoya, Santander, Colombia.

TYPE MATERIAL.—The female holotype, male allotype, and 90 paratypes were taken at the type locality on 2-VII-1970, 150 m, No. 590, from tree branches (Fabaceae ?), by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes tardus, n. sp.

This species is distinguished from the remotely related *imitans* (Eggers) by the very different female frons as described below, by the less strongly arched pronotum, by the more elongate elytra, by the less strongly convex declivity, and by other characters.

FEMALE.—Length 2.3 mm, 2.3 times as long as wide; color yellowish brown.

Frons moderately convex, protruding slightly on median fourth toward epistoma; median third smooth, brightly shining, impunctate from epistoma three-fourths distance to upper level of eyes, lateral and dorsal margins with fine punctures and ornamented by moderately sparse, very long, golden hair, tips of longest dorsal setae almost reach epistoma; scape with a small tuft of long hair.

Pronotum 1.0 times as long as wide; resembling *imitans* except basal two-thirds less strongly arched, surface dull, reticulate, punctures larger.

Elytra 1.4 times as long as wide, 1.4 times as long as pronotum; resembling *imitans* except disc not arched, declivity steeper, somewhat flattened, interstrial setae on disc slightly longer and slightly stouter on declivity; declivital interstriae 10 continuing to apex, rather broad, not carinate.

TYPE LOCALITY.—Piedras Blancas, 10 km east of Medellin, Antioquia, Colombia.

TYPE MATERIAL.—The female holotype and one broken female paratype were taken at the type locality on 15-VII-1970, 2500 m, No. 684, from *Clusia*, by me.

The holotype and paratype are in my collection.

Scolytodes vesculus, n. sp.

This species is distinguished from *libidus* Wood by the larger size, by the slightly smaller pronotal and elytral punctures, by the longer pubescence on the pronotum and elytral disc, and by other minor characters cited below.

MALE.—Length 1.3 mm (paratypes 1.3–1.5 mm), 2.2 times as long as wide; color very dark brown.

Frons as in *libidus* except punctures smaller.

Pronotum as in *libidus* except anterior margin without a definite row of serrations, punctures smaller (their lateral margins not raised or with a small shining spot), setae very fine, longer, apparently more abundant.

Elytra as in *libidus* except punctures much smaller, striae rows usually not evident, erect setae similar but recumbent setae distinctly longer.

TYPE LOCALITY.—Piedras Blancas, 10 km east of Medellin, Antioquia, Colombia.

TYPE MATERIAL.—The male holotype and two male paratypes were taken at the type locality on 15-VII-1970, 2500 m, No. 678, from *Croton guianensis*, by me.

The holotype and paratypes are in my collection.

REPTILE POPULATION CHANGES WITH MANIPULATION OF SONORAN DESERT SHRUB

David J. Germano¹ and C. Roger Hungerford¹

ABSTRACT.— The diversity and abundance of reptiles were studied in three vegetation types on the Santa Rita Experimental Range, Arizona. Total reptile sightings were greatest in undisturbed mesquite and mesquite with irregularly shaped clearings. No zebra-tailed lizards (*Callisaurus draconoides*) or desert spiny lizards (*Sceloporus magister*) were seen, and significantly fewer western whiptails (*Cnemidophorus tigris*) were in the mesquite-free area. Only the Sonora spotted whiptail (*Cnemidophorus sonorae*) was significantly more abundant in the mesquite-free area than in the undisturbed mesquite. In an effort to increase grass production for cattle in mesquite grasslands, it is preferable to clear irregularly shaped areas rather than to attempt total mesquite removal, if reptiles are to be considered.

Desert grasslands of the southwestern United States have been invaded by stands of mesquite (*Prosopis juliflora*) during the last 100 years (Martin and Reynolds 1973, Martin 1975). As the mesquite increased, grass production decreased (Parker and Martin 1952, Caraher 1970). Traditional use of these lands has been for grazing domestic animals. To increase grass production for cattle on these ranges, much of the mesquite is being eliminated. This vegetation conversion to grass also occurs in other vegetation types such as sagebrush and pinyon-juniper. In past years the impact of vegetation manipulation on economically important wildlife species was studied. The current total ecosystem approach includes the investigation of the impact of these practices on all life forms. This paper presents one advantage of this approach.

Because of the smaller size and lower mobility of reptiles, their diversity is more closely tied to vegetation diversity than is that of large mammals and birds. Some reptiles are adapted to dense grass areas, some to life in trees, some to sandy substrates, etc. Environments can be stratified in a vertical direction and a horizontal direction, creating many habitats for a variety of reptile species. A uniform stand of grass may offer only a few habitats in a horizontal direction and none in the vertical direction. But a mesquite-grassland environment offers several strata

vertically that can be exploited by several species. For example, the vegetation is more dispersed horizontally and may offer many habitats. Mesquite trees inhibit the growth of other vegetation under them, creating bare ground and litter areas. Sandy areas in adjacent washes may provide yet another habitat for reptiles. By clearing only patches in mesquite, it may be possible to increase grass growth and also maintain a greater variety of reptile species at the same time.

The purpose of this study was to monitor reptile responses to the creation of irregularly shaped clearings in mesquite on desert grassland range. Mammal and bird response is reported elsewhere.

ACKNOWLEDGMENTS

We acknowledge the assistance of Robert O. Kuehl for his suggestions on the analysis of the data and, also, the assistance of S. Clark Martin and Norman S. Smith during this study. We thank the U.S. Forest Service, Rocky Mountain Forest and Range Experiment Station, for allowing us to use the Santa Rita Experimental Range for this study.

STUDY AREA

The Santa Rita Experimental Range, 48 km south of Tucson, Arizona, is a 20,250 hectare area set aside for study since 1903

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(Martin and Reynolds 1973). Local ranchers have been allowed to graze their cattle on these ranges but only in conjunction with grazing systems designated by the U.S. Forest Service, which administers the Experimental Range. The Experimental Range does not receive the man use that other similar non-protected areas receive. Hunting is restricted on the range and off-road vehicle use is prohibited. Many of the vegetation changes occurring on the range are well documented since the early 1900s, which, although incomplete, forms a basis for future ecosystem studies.

The climate of the range is typical of the semiarid Southwest, with low relative humidity and daily temperatures sometimes exceeding 38 C during the summer. Average annual precipitation in the study pastures ranges from 35 to 40 cm. About 60 percent of the annual moisture falls during the summer rainy season and produces most of the perennial grasses. Effective rainfall is unusual in April-June, the driest part of the year. The major shrubs are mesquite, cacti (*Opuntia spp.*), and burroweed (*Haplopappus tenuisectus*) (Martin and Reynolds 1973).

Observations were made in the three pastures from April to September 1977 and April to June 1978. The mesquite stand was undisturbed in one pasture (undisturbed mesquite); seven spot clearings ranging from 3 to 30 hectares were established in the second pasture (mesquite with clearings) by chaining in July 1976; mesquite in the third pasture (mesquite-free) was killed with diesel oil in 1955 (Fig. 1).

Cattle grazed the study pastures in a one-herd, three-pasture, three-year rotation. In each three-year cycle each pasture was grazed once November through February and once March through October, with 12 months of rest following each grazing period.

METHODS

We established four census lines, each 1200 m long, perpendicular to the drainage patterns in each pasture. Every reptile found was censused. Six species, zebra-tailed lizard (*Callisaurus draconoides*), desert spiny lizard (*Sceloporus magister*), lesser earless lizard (*Holbrookia maculata*), tree lizard (*Urosaurus inornata*), western whiptail (*Cnemidophorus*

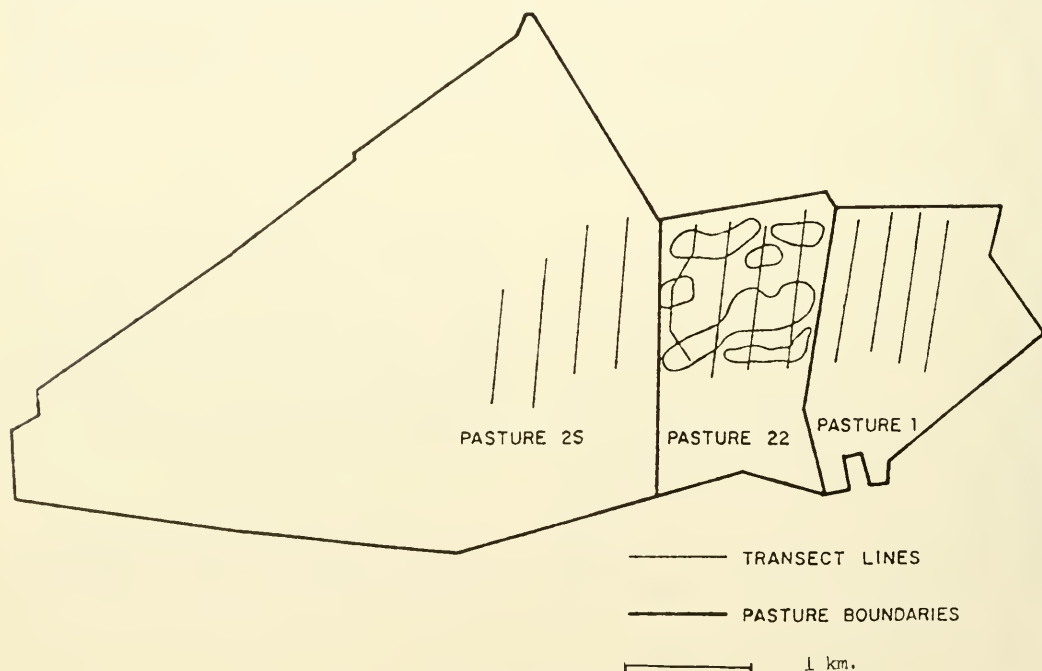


Fig. 1. The three pastures used in the study, showing placement of transect lines and size and shape of the seven clearings in pasture 22.

tigris), and Sonora spotted whiptail (*C. sonorae*), were found in sufficient numbers to analyze statistically. No effort was made to census nocturnal reptiles, a fact that accounts for the few snake sightings. Reptiles were censused by recording every reptile seen while walking the transect lines. Two transect lines were walked each morning, for six mornings, each month of the study. The actual morning starting time varied each month that we censused diurnal reptiles. Pianka (1970) notes that whiptails exhibit unimodal activity in the spring and bimodal activity in the summer, a habit directly related to soil temperatures. Milstead (1957) found whiptail activity began in the morning when soil temperatures reached 50–52 C. The same is true of other lizards; consequently, we began censusing earlier in the morning from June on, as compared to April and May. We therefore censused during peak lizard activity, using 7 × 35 binoculars to identify all reptiles seen.

Because the data were not normally distributed, we used a method (Bhappkar 1968) that categorizes the data into counts per transect to test for significant differences ($P<.05$). To test for significant differences

between treatments, we used the “least significant difference” method ($P<.05$) (Steel and Torrie 1960). To test for differences between the number of reptiles visually censused in the mesquite and the number in the clearings of the second pasture, we used the nonparametric sign test ($P<.05$) (Steel and Torrie 1960).

RESULTS AND DISCUSSION

The number of desert spiny lizards, lesser earless lizards, and unidentified lizards seen showed no significant differences between treatment areas (Table 1).

The zebra-tailed lizard was seen significantly more often in the undisturbed mesquite pasture than in either the mesquite with clearings or the mesquite-free pasture. The tree lizard was seen significantly more often in the mesquite with clearings than in either of the other pastures. Western whiptails were seen significantly more often in the pastures containing mesquite than in the mesquite-free pasture. Only the Sonora spotted whiptail was seen more often in the mesquite-free pasture than in the mesquite

TABLE 1. The number of reptiles sighted, number of counts per transect (mean score), and variance for each treatment and chi-square (X^2) value for each species using the method developed by Bhappkar (1968). Each treatment has two degrees of freedom. (Significant differences ($P<.05$) in numbers on the same line are indicated by suffixes that do not include a common letter.)

Species	Number sighted	Vegetative characteristics									X ²
		Mesquite with clearings			Undisturbed mesquite			Mesquite-free			
		Mean score	Variance	Number sighted	Mean score	Variance	Number sighted	Mean score	Variance		
Zebra-tailed lizard		20 ^b	0.278	0.023	61 ^a	1.694	0.038	0 ^b	0	0	32.869*
Desert spiny lizard		5	0.139	0.003	12	0.333	0.031	0	0	0	1.107
Lesser earless lizard		31	0.861	0.023	18	0.500	0.021	22	0.611	0.016	3.101
Tree lizard		42 ^a	1.167	0.073	16 ^b	0.444	0.012	22 ^b	0.611	0.031	6.232*
Western whiptail		210 ^a	5.833	0.970	303 ^a	8.417	1.670	3	0.083	0.002	73.454*
Sonora spotted whiptail		53 ^a	1.472	0.081	8 ^b	0.222	0.005	70 ^a	1.944	0.148	35.984*
Leopard lizard		1			1			0			
Eastern fence lizard		0			0			1			
Regal horned lizard		0			1			0			
Sceloporus spp.		2			3			1			
Cnemidophorus spp.		17			7			9			
Unidentified lizard		41	1.139	0.057	30	0.833	0.033	55	1.528	0.073	4.657
Western diamondback rattlesnake		0			0			1			
Unidentified snake		0			0			1			
Western box turtle		0			0			2			
Western spadefoot		0			0			1			
All reptiles		422 ^a	11.722	2.293	460 ^a	12.056	2.444	188 ^b	5.194	0.674	10.597*

°Significant difference ($P<.05$)

pastures, and these differences were statistically significant only as compared to the undisturbed mesquite pasture. The Sonora spotted whiptail was also seen significantly more often in the mesquite with clearings than in the undisturbed mesquite (Table 1).

When comparing the spot clearings with the mesquite areas of the mesquite with clearings pasture, there were significantly more tree lizards in clearings and significantly more zebra-tailed lizards in the mesquite (Table 2). We believe this unexpected result was due to specific microhabitat preferences for each species. These are discussed more fully below in each species account.

The graph showing the total sightings of all reptiles by month (Fig. 2) illustrates lizard preferences for areas with mesquite. Except in April and June 1977, every month we saw at least twice the number of reptiles in the pastures with mesquite as the mesquite-free pasture. May of each year showed high numbers not only for total reptile sightings but also for individual species (Figs. 2-7). May is the first month on the range where temperatures are consistently high and most reptiles have emerged from winter torpor to resume feeding. June of both years brought a drop in numbers for total reptile sightings (Fig. 2). Western whiptails and lesser earless lizards also showed this reaction (Figs. 4 and 6). June is the hottest, driest month of the year. Zebra-tailed lizards in the undisturbed mesquite showed little fluctuation throughout their active period (Fig. 3). The spring of 1978 showed increased numbers in all species and total sightings of all reptiles, possibly due to the very wet winter experienced in 1977-78 (Figs. 2-7).

Zebra-tailed lizard

The undisturbed mesquite range contained significantly more zebra-tailed lizards than the mesquite-free range. In fact, there were none in the mesquite-free range. They utilize a wide variety of habitats in the arid Southwest, including washes, flood plains of rivers, sand dunes, and flat land deserts (Vitt and Ohmart 1977a). They are particularly associated with open space where they can run between shrubs (Pianka and Parker 1972, Tanner and Krogh 1975). These conditions are met by the mesquite areas where large sandy washes are found and the vegetation around the mesquite is sparse with many open areas. On the mesquite-free range, the drainages were not sandy but were covered with grasses and forbes. Also, there were no open spaces between shrubs because of the dense grass growth. In the mesquite with clearings the zebra-tailed lizards were only seen in the mesquite areas, usually in the sandy washes. It is insectivorous (Kay et al. 1970), often feeding on insects found on either overhanging annual vegetation or overhanging perennials such as catclaw and mesquite (Vitt and Ohmart 1977a). A mesquite-free range in which grasses dominate would eliminate zebra-tailed lizard populations.

Desert Spiny Lizard

The authors found no significant difference between pastures for this lizard, possibly due to the nature of the test used. There were none in the mesquite-free range. Desert spiny lizards are primarily arboreal on cottonwoods, mesquite, and willows. Parker and

TABLE 2. The number of reptiles sighted in the two habitat types of the mesquite with clearings pasture, the mean (\bar{X}), standard deviation (S), and Z score using the nonparametric sign test. (Significant differences ($P < .05$) in numbers on the same line are indicated by suffixes that do not include a common letter.)

Species	Vegetative characteristics				
	Mesquite	Clearings	\bar{X}	S	Z
Zebra-tailed lizard	18 ^a	2 ^b	5.5	1.658	3.016*
Desert spiny lizard	4	1	2.5	1.118	0.894
Lesser earless lizard	15	16	8.5	2.062	0
Tree lizard	9 ^a	33 ^b	9.0	2.121	2.122*
Western whiptail	102	108	14	2.646	0.945
Sonora spotted whiptail	34	19	8.5	2.062	0.485

*Significant difference ($P < .05$).

Pianka (1973) often found them in trees that had pack rat nests at their bases. We also observed this on the pastures with mesquite. These lizards were quite wary and often would jump out of a mesquite tree, as high as 5-6 feet from the ground, and run down a hole in a pack rat nest. As with the zebra-tailed lizard, a mesquite-free environment would not provide the habitat needed by desert spiny lizards. Mesquite remaining from spot clearing will provide the necessary habitat for desert spiny lizards.

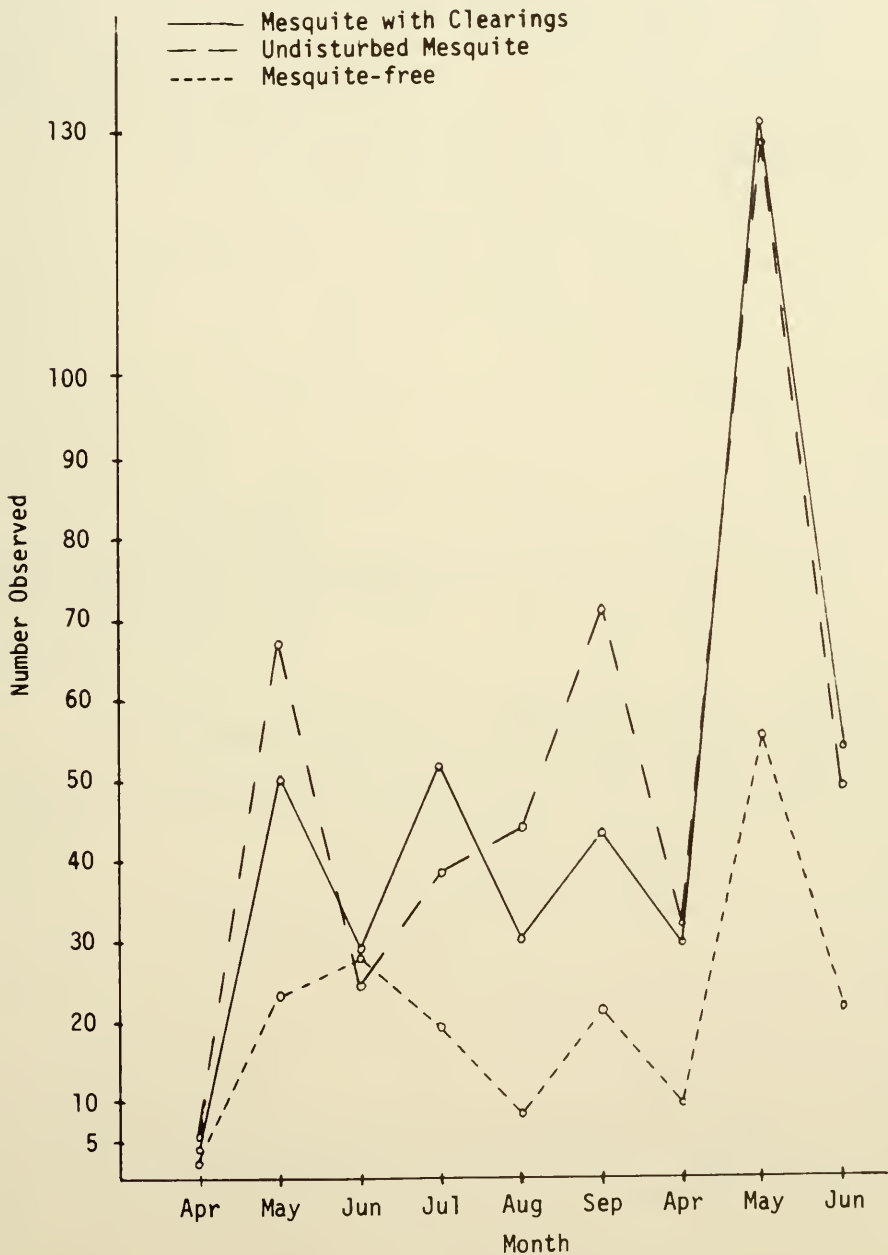


Fig. 2. Sightings of all reptiles by month, April-September 1977 and April-June 1978.

Lesser Earless Lizard

We found no significant differences between pastures in the number of lesser earless lizards seen. We also saw no significant difference in their sightings between the mesquite and the clearings of pasture 22. A slight trend of higher numbers can be seen in the graph for 1978 for the mesquite with clearings, but numbers and length of time observed are not enough to be conclusive. Further study of this trend may show a preference for the mesquite habitat with clearings. Gennaro (1972) found that the lesser earless lizard fed in open areas with sparse

vegetation. Degenhardt (1966), working in the Big Bend National Park in Texas, found that the lesser earless lizard seemed to prefer flat areas with sparse vegetation. This did not occur in our study area. The lesser earless lizard was seen approximately as often in the dense grass areas as in the areas with sparse vegetation. Stebbins (1966) shows that the lesser earless lizard occupies a wide range of habitats, including washes, sandy stream banks, sand dunes, short grass prairies, mesquite woodlands, and farmlands. The lesser earless lizard apparently would not decrease significantly in numbers if mesquite were totally removed.

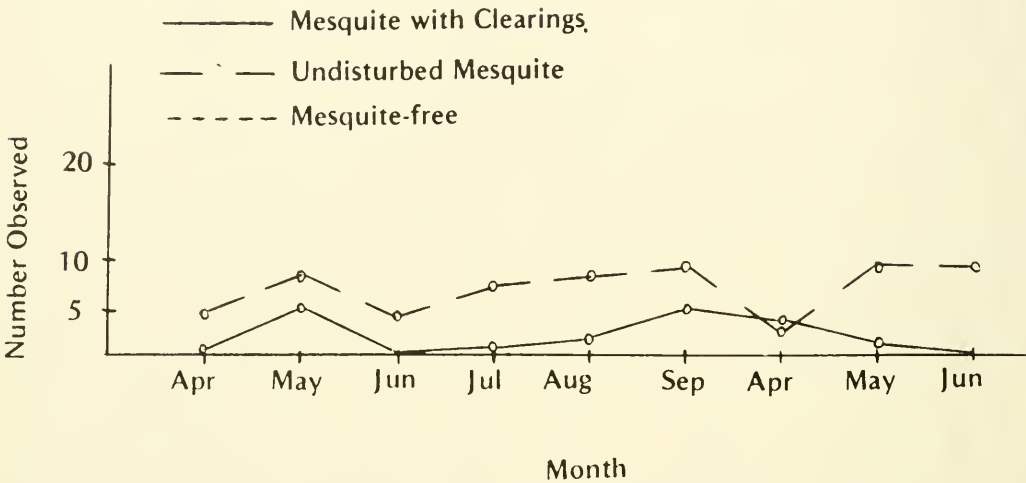


Fig. 3. Sightings of zebra-tailed lizards by month, April–September 1977 and April–June 1978.

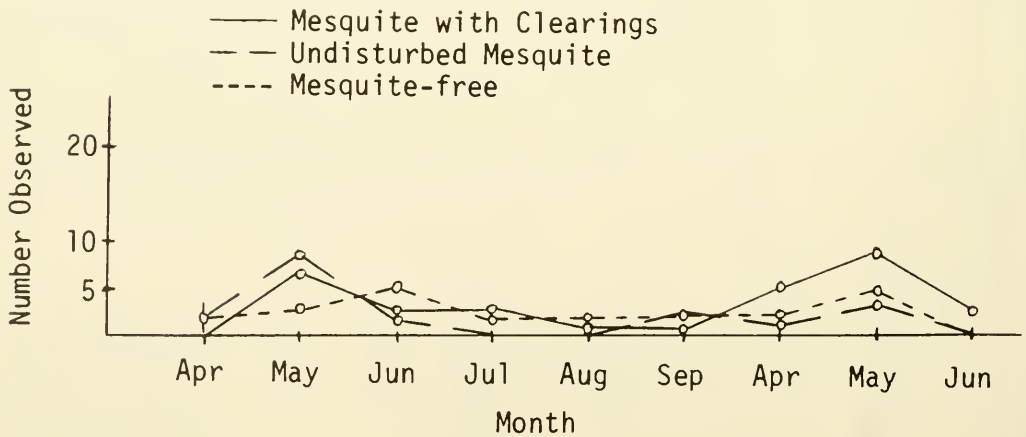


Fig. 4. Sightings of lesser earless lizards by month, April–September 1977 and April–June 1978.

Tree Lizard

Tree lizards were significantly more abundant in the mesquite with clearings pasture than the undisturbed mesquite pasture. They are found in a variety of habitats but are mostly arboreal (Aspland 1964). They are rarely found in areas where trees are absent and then usually in rocky terrain (Aspland 1964, Milstead 1970). We found about the same number in the mesquite-free pasture as the undisturbed mesquite pasture. This may have been partially due to our inability to see the tree lizards on mesquite trees as often as they occurred. Tree lizards are cryptically colored and patterned and, without movement on their part, they are difficult to detect. On the mesquite-free range, we saw them often on stumps of dead mesquite. We saw significantly more tree lizards in the clearings than in the mesquite of pasture 22, and almost always on the fallen dead mesquite. In winter, tree lizards often aggregate in large numbers under the loose bark of dead mesquite (Vitt 1974). Also, the termite *Kaloterms minor* is often a prey item commonly found in standing or fallen dry wood (Aspland 1964). The dry mesquite in pasture 22 is a source of both food and hibernating sites for tree lizards and probably is the reason we found significantly more tree lizards in this pasture.

Western Whiptail

The authors saw significantly more western whiptails in the mesquite pastures than in

the mesquite-free pasture. Of 516 western whiptails seen, only three were in the mesquite-free pasture. Western whiptails inhabit xeric habitats (Medica 1967), often with sparse vegetation and open areas (Burkholder and Walker 1973, Schall 1977). They forage in shrubs and run swiftly between these shrubs (Vitt and Ohmart 1977b). Their food consists largely of termites (Echternacht 1967, Pianka 1970). The dense grasses of mesquite-free pasture hinders both movements and foraging behavior of the western whiptail. A significant difference was not found between the number of western whiptails seen in the clearings and in the mesquite of pasture 22. Overall, however, western whiptails should be found in good numbers in the mesquite left from spot clearing.

Sonora Spotted Whiptail

The other whiptail species we found is probably the Sonora spotted whiptail as defined by Lowe and Wright (1964), but some nonwestern whiptails seen may be hybrids of the bisexual western whiptail and the parthenogenic Sonora spotted whiptail (Lowe et al. 1970). The name Sonora spotted whiptail designates the whiptails seen that were not western whiptails.

Both the mesquite-free and the mesquite with clearings pastures contained significantly more Sonora spotted whiptails than the undisturbed mesquite pasture. The Sonora spotted whiptail is found in the southeast corner of Arizona, with the Chihuahua whiptail (*Cnemidophorus exsanguis*) occurring in

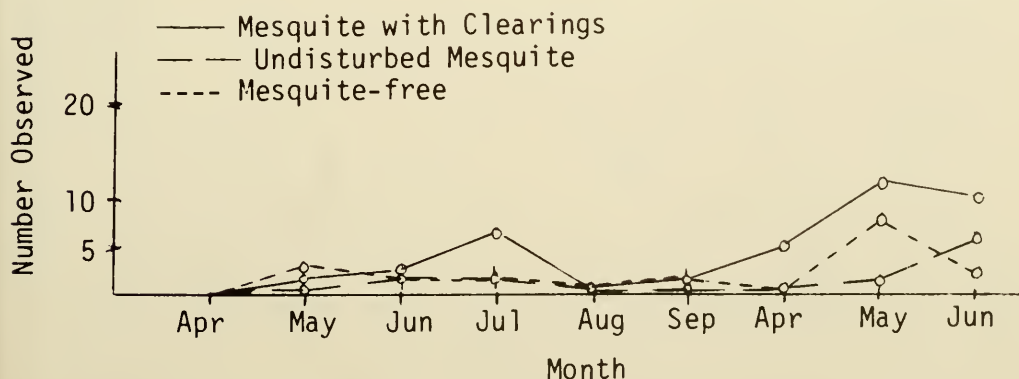


Fig. 5. Sightings of tree lizards by month, April–September 1977 and April–June 1978.

Arizona only near the Arizona-New Mexico border (Wright and Lowe 1968). Echternacht (1967), working on the Santa Rita Experimental Range, found what he called the Chihuahua whiptail (more likely the Sonora spotted lizard) at higher elevations but not in the grasslands. He thought their numbers diminished as the elevation lowered. Wright and Lowe (1968) indicate the Sonora spotted whiptail's habitat as essentially woodlands,

with local populations occurring in desert-grassland and desert scrub. This lizard is found between 1065 and 2130 m (Lowe and Wright 1964), but we found more of them as the elevation increased. We also found no significant difference in the number seen between the mesquite and the openings of the mesquite with clearings pasture, a fact indicating no habitat preference. At elevations where Sonora spotted whiptails do occur,

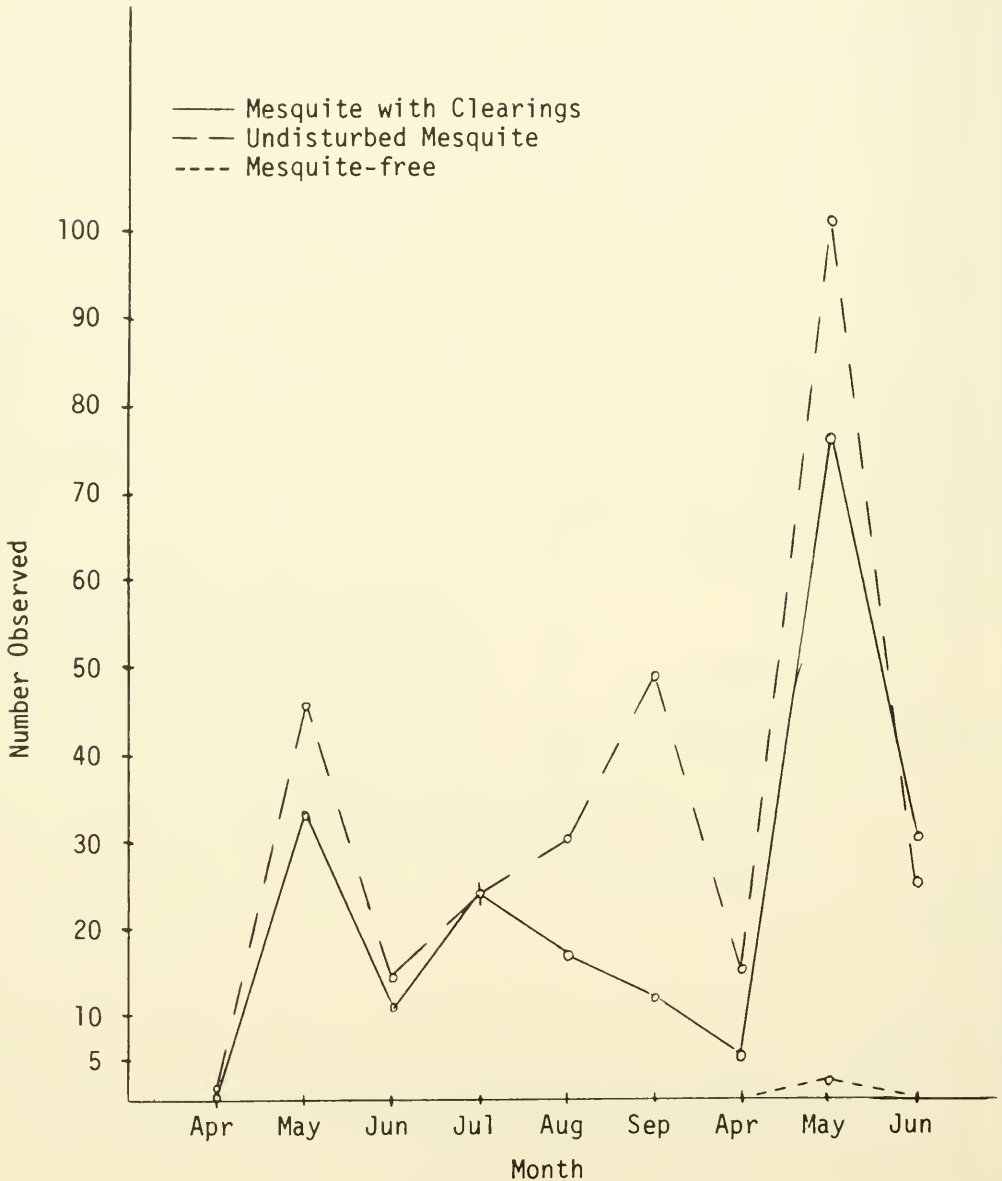


Fig. 6. Sightings of western whiptails by month, April–September 1977 and April–June 1978.

clearings in mesquite would not be harmful to their populations.

SUMMARY

Partial clearing of mesquite was less detrimental to the lizards observed than was complete clearing. For the tree lizard there was a definite benefit in having spot clearings with the dead mesquite left in the clearings. Although the mesquite-free pasture contained a few species not seen in the other two pastures, they were seen in such low numbers that no conclusions could be made.

Even in an area that is mostly grass there will probably remain horizontal stratification. This can occur and did occur on our study area where hillsides were rocky and where patches of bare ground were evident. Grasslands, though, lack the vertical stratification necessary for arboreal species. We did see an eastern fence lizard and an unidentified *Sceloporus*, but these were on remnant mesquite at the border of the pasture and would not be expected to occur if vast areas of mesquite were converted back to grasslands. The mesquite-free areas contained few to no zebra-tailed lizards, desert spiny lizards, or western whiptails, all of which were found in partially cleared mesquite.

Spot clearing in mesquite resulted in greater diversity of habitat, less visual impact than did total clearing of mesquite, was less detrimental to reptiles, and still increased forage production for livestock. More lizard species should be found as the environment becomes more complex. Proper location of clearings could accomplish the range management objectives while causing the least amount of disturbance to existing reptile populations. There is even the potential of an increased diversity of lizard species as clearings in mesquite are opened to allow for the dense growth of grass while retaining the habitats found in mesquite woodlands.

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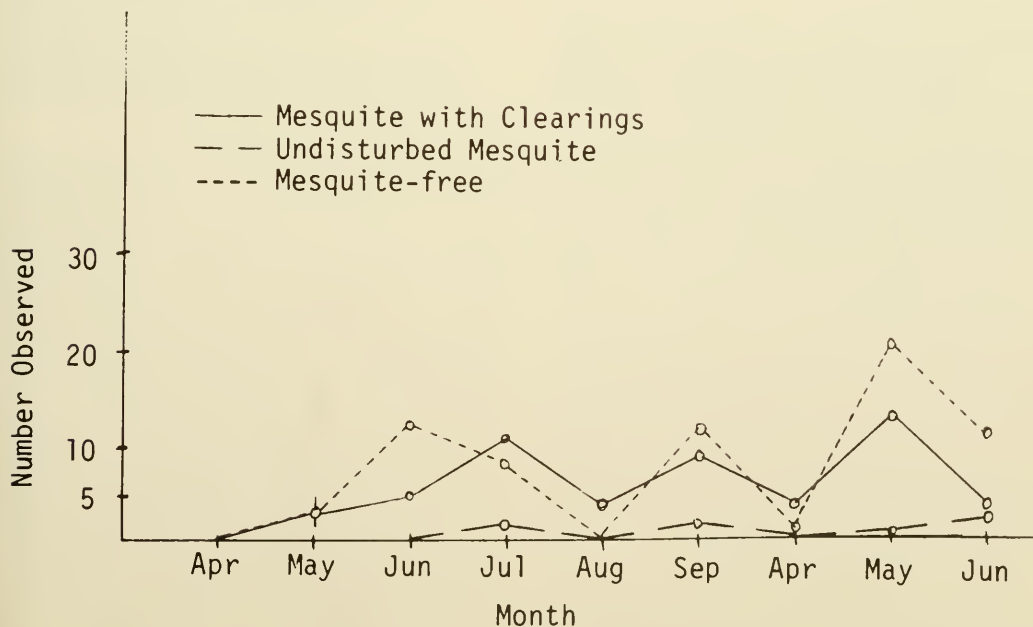


Fig. 7.—Sightings of Sonora spotted whiptails by month, April–September 1977 and April–June 1978.

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A NEW *HYPSIGLENA* FROM TIBURON ISLAND, SONORA, MEXICO

Wilmer W. Tanner¹

ABSTRACT.—*Hypsiglena torquata tiburonensis* is described as new to science from Isla del Tiburon, Sonora, Mexico. Notes pertaining to other taxa in the genus are included.

The islands in the Gulf of California continue to produce interesting variations in the genus *Hypsiglena*. Few islands are without representatives of the genus and all island populations show some variations not found in Baja California or Sonora populations. Those islands furthest from the coast and off the coastal shelf, such as Tortuga and Santa Catalina, show the most variation, an indication of their longer isolation.

A most unusual pair of specimens is available from the island of Tiburon. They are unusual in their color pattern and particularly in the large number of dorsal spots. As noted above, it is not unexpected for island populations to be differentiated from the mainland populations, but, considering the short distance from costal Sonora to Tiburon, one would not expect such a radical departure in pattern. Because the population is distinct, I choose to name it—

Hypsiglena torquata tiburonensis, n. subsp.

Fig. 1

HOLOTYPE.—An adult female, BYU 33181, taken by James R. Dixon, on Isla del Tiburon, Sonora, Mexico, 14 August 1974.

PARATYPE.—An adult female, MVZ 37802, taken by C. G. Sibley at Ensenada del Perro, Isla del Tiburon, 10 November 1941.

DIAGNOSIS.—A subspecies of *Hypsiglena torquata* characterized by light brown spots, which are narrowly separated from one another (usually less than one scale) and involving 7–9 dorsal scale rows. There is a strong tendency for the dorsal spots to be separated or only narrowly connected at the dorsal midline. In the holotype, the nape pat-

tern is similar to *deserticola*, but in the paratype it is as in northern Sonora and Arizona specimens. The subspecies *tiburonensis* is most closely related to those nearby populations in Sonora and Arizona and in the Great Basin, but it is distinct in the number, size, and shape of the dorsal spots.

DESCRIPTION.—Rostral broad, rounded, and projecting anteriorly 0.7 mm, 17.5 percent of distance to anterior edge of frontal; loreals 1-1; preoculars 2-2; temporals 1-2; supralabials 8-8; infralabials 10-10, four rows of gulars between posterior chinshields and first ventral; ventrals 185; caudals 52; anal divided; dorsal scales in 21-21-15 longitudinal rows.

Nape pattern of three dark blotches, the median one of these with three parts, the anterior median portion narrow, extending from the parietal posteriorly 5 scales to fuse on each side with the lateral portions of this spot; lateral nape spots separated from median and extending anteriorly to orbit; dorsal blotches on body 86, many divided or narrowly connected medially, spots separated by narrow pale cross-bands usually one-half scale wide, dorsal spots when united forming a band across dorsum involving 7–9 scale rows. Dorsum of head without dark spots; body color a light brown with narrow, cream-colored mottling separating the spots.

MEASUREMENTS.—Snout-vent length 376 mm; tail length 68 mm; tail 15.3 percent of total length; head length, from snout to posterior edge of parietals 11.4 mm; head width 10.5 mm; diameter of eye 2.1 mm.

REMARKS.—The size, shape, and number of dorsal body spots is the most distinctive character in *tiburonensis*. There are other sub-

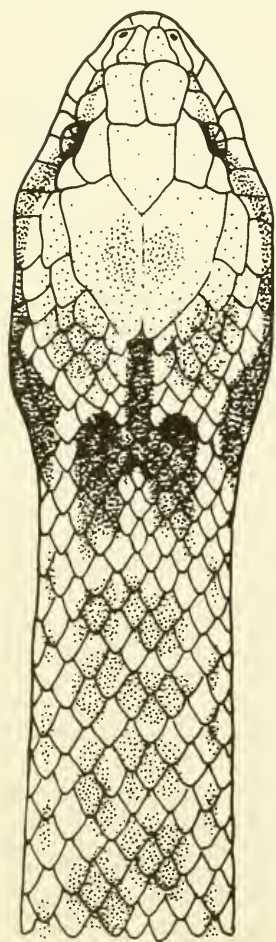
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species with dorsal spots that extend across the dorsum to occupy 7–9 rows of scales (*t. torquata*, *t. nuchulata*, *t. baueri*), and perhaps occasional specimens in other subspecies, but in these the spots are longer; that is, they involve 2–3 or more scale lengths. In *tiburonensis* the dorsal spots are less than 2 scales and usually $1\frac{1}{2}$. The pale bands between the dorsal spots are narrow, less than one scale length; thus, the narrow spots and interspaces provide space for more spots, characteristic of this subspecies. In *t. venusta* there are large numbers of dorsal spots (69–95); however, they are small, divided middorsally to form two rows that extend for most or all the body length and involve only 2–3 rows of scales. Furthermore, they are, as in *tiburonensis*, narrowly divided by lighter cross-bands between the spots (Tanner 1944

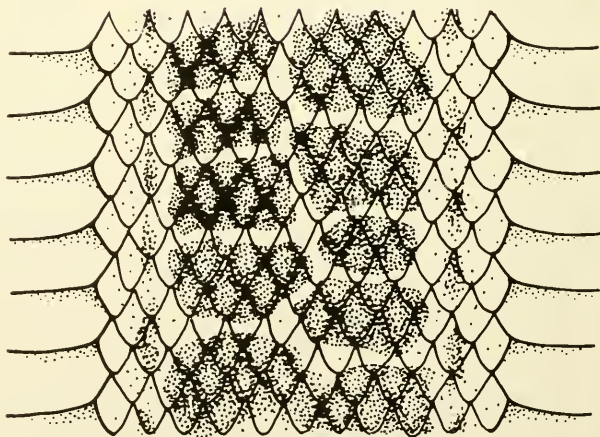
[1946]). Although the nape pattern is similar to that of *deserticola*, it does have its own uniqueness and appears to consist basically of three narrowly fused spots.

A series of 10 females from Sonora provides little scutellation variation between them and *tiburonensis*, with ventral means 183.3 to 182.5, respectively. The caudals are also close, with means of 55 to 52, respectively (the paratype is missing its tail tip). The greatest variation between Sonora and Tiburon specimens occur in the number of dorsal body spots, with females having 59.1 to 77.5, respectively.

It should be noted again that the series from Sonora includes both those specimens showing a pale nape band (typical *torquata*), and those representing the northern type (*ochrorhynchus*), all of which are without any



A



B

Fig. 1. *Hypsiglena torquata tortugaensis*, BYU 33181, holotype: A, head and nape patterns; B, dorsal spots.

remnant of the white band. In the *torquata* dorsal body pattern, the pale areas that divide the dark dorsal spots are narrow, as in *tiburonensis*, but otherwise the pattern is very different with fewer, larger, and broader spots. In the specimens from northern Sonora and most of adjoining Arizona, northwestern Chihuahua, and extreme south-central Utah, the light areas between the spots are wider, covering one or more scales. The nape pattern in the northern populations is usually a fusion of the spots to form an irregular dark brown band that laterally extends anteriorly to the orbits; or the nape pattern may have a central elongate spot extending posteriorly from the parietals for approximately 7–10 scales and, at its widest, 3–4 scales wide. In some specimens the median spot is fused on one side with a lateral nape spot. In all specimens examined, the lateral spots extend to the orbit.

Based on color pattern, the relationship of *tiburonensis* is closer to those populations in northwestern Sonora and those further to the north, including *deserticola* (which has a similar nape pattern). There is also a general lightening of the brown color and a strong tendency for scales in the dorsal blotches to be edged with dark, its centers being a lighter brown. This lightening seems to be true for desert populations, but a darker brown is present in most areas where an increase of moisture occurs. Three specimens from San Esteban Island (CAS-SU-9038, UM 128641, and MVZ 74953) are similar to *tiburonensis* in having numerous dorsal body spots, 90, 78, and 82, respectively. Other characters are also similar, such as ventrals, ♀ 184–186, and caudals, 46–52; one male has 173 ventrals and 55 caudals. The similarities between these two island populations dictate that they should be included in the same taxon, at least until larger series from each island warrant a separation.

An examination of specimens from adjoining Sonora showed little similarity in color pattern. As noted above, the nape pattern was similar to *t. deserticola* and the scale patterns were almost identical to the Sonora and Arizona specimens. An examination of the Sonoran specimens available to me shows as great a color pattern variation as in any other geographical area, except perhaps Baja

California. It is in Sonora that the light, cream-colored nape band disappears and the dark nape pattern becomes an irregular band or three nape spots. An occasional specimen from southeastern Sonora and adjoining southwestern Chihuahua has a much broader, more uniform dark band.

It was from this general area and on the basis of comparisons with more southern populations that Dunn (1936) synonymised *ochrorhyncha* with *torquata*, this in spite of the very few specimens available and in contrast to the Stejneger and Barbour (1917) assignment. Both Tanner (1946) and Dixon (1965 and 1967) accepted *ochrorhyncha* based on the distinct color pattern of limited specimens available between typical specimens of the two types. With a substantial increase in the numbers of specimens throughout the entire range of *Hypsiglena*, it is now generally agreed that only one widespread species (*torquata*) is assignable to the genus *Hypsiglena* (Tanner 1954, 1958, 1960, 1962, 1963, 1960, 1966, Schmidt 1953, Bogert and Oliver 1945, Zweifel and Norris 1955, Smith and VanGelder 1955, Duellman 1957, Fugler and Dixon 1961, Fouquette and Rossman 1963, Hardy and McDiarmid 1969).

Dixon and Lieb (1972) described as a new species *Hypsiglena tanzeri*. Based on the description, figures, and my examination of the paratype (LACM 72068), it appears to be a color variation of *torquata* and should thus be considered a unique subspecies of *torquata*. An examination of *t. tanzeri* places it as one color pattern extreme in the large size and small number of body spots; *t. venusta* is the other extreme. In *Hypsiglena*, the size, shape, and number (now known to range from 37–95) of body spots and the nape pattern are highly variable. This character alone, I believe, does not warrant species status for *tanzeri*. This wide range of color pattern variation I consider particularly characteristic in *Hypsiglena*. Tanner, Dixon, and Harris (1972) found in *Crotalus lepidus* an extreme color pattern modification in which the dark body bands were reduced in *l. maculatus* to dorsal spots, the smaller cross bands appearing on the posterior third of the body. This same pattern occurs in *t. tanzeri*, with the more typical spots occurring posteriorly. Such extensive color pattern variations have also

been found to occur in such species as *Sonora semiannulata* and *Lampropeltis getulus*.

Hypsiglena specimens are available to me from the following Gulf of California islands: Angel de La Guarda, Danzante, Partida (Norte), Partida (Sur), Mejiia, Santa Catalina, San Francisco, San Esteban, San Jose, Monserrate, San Lorenzo, San Marcos, Tiburon, and Tortuga. On each of those islands *Uta* is abundant, and on most *Cnemidophorus* is present. Small lizards, particularly *Uta*, are the food sources for *Hypsiglena*. This predator-prey relationship is widespread in western North America and is particularly so on these islands. This predator-prey relationship occurs on the islands of Cedros and San Martin on the Pacific side of the Baja Peninsula and most likely occurs on all islands of the area. It is suspected, therefore, that if *Uta* is present, *Hypsiglena* will also be there.

ACKNOWLEDGMENTS

Several individuals have aided in providing materials for this study. I am grateful to Dr. Alan Levitan (CAS), Dr. Robert Stebbins (MUZ), and Dr. Arnold Kluge (UM) for the loan of specimens and to John Ottley and his companions for the considerable field work done in Mexico during the past decade.

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ERIOGONUM DIVARICATUM HOOK. (POLYGONACEAE),
AN INTERMOUNTAIN SPECIES IN ARGENTINA

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ABSTRACT.—*Eriogonum divaricatum*, an annual herb of clay slopes and flats in the Green and Colorado river drainage basin of the western United States, was found at the turn of the century in three locations in southern Argentina. The South American material was described in 1902 as a new species of *Eriogonum*, *E. ameghinoi* Speg., and this name was the basionym for a new monotypic genus, *Sanmartinia* M. Buchinger, proposed in 1950. The species has not been rediscovered in Argentina, and the presence of the species in South America was probably the result of a long-distance dispersal event involving shore birds.

With the publication of *Eriogonum ameghinoi* Speg. (Spegazzini 1902), *Eriogonum* Michx. (Polygonaceae), long considered restricted to Canada, United States, and Mexico, became defined as a taxon found in both North and South America. When Buchinger (1950) based the monotypic *Sanmartinia* on *E. ameghinoi*, *Eriogonum* was once again defined as endemic to North America. Other genera belonging to the subfamily Eriogonoideae are present in Chile and Argentina, namely *Chorizanthe* R. Br. ex Benth. (Goodman 1934), *Oxytheca* Nutt. (Ertter 1980), and *Lastarriaea* Remy (Goodman 1934). All are related to *Eriogonum* but differ in having barbed or otherwise armed involucre or tepals. This morphological feature has been suggested as the means for dispersal by animals from arid regions in western North America to similar areas in southern South America (Reveal 1978). I have proposed (Reveal 1978) two separate occasions of migration. The first involved the perennial species of *Chorizanthe* now found in South America that came from the then perennial members of the genus in North America (now extinct in the north and replaced by annual species). The second migration that occurred probably happened much later (probably during the Pleistocene), and this resulted in the introduction of an array of annual species into South America, notably *O. dendroidea* Nutt. ssp. *chiliensis* (Remy) Ertter, *C. commissuralis* Remy, and probably *L. chiliensis* Remy. In each of these

cases, the migration was a success and colonization occurred.

My own views regarding *Sanmartinia* have been largely masked in ignorance of the exact nature of the material. In my doctoral dissertation (Reveal 1969), *Eriogonum ameghinoi* was excluded from the genus and placed in *Sanmartinia*. This view persisted until publication of the excellent paper by Moreau and Crespo (1969). They noted that the supposed lack of an involucre, as suggested by I. M. Johnston on an annotation attached to one of the Ameghino specimens, badly misled Buchinger, and the species was not representative of a new genus but a typical species of *Eriogonum*.

Unfortunately, Moreau and Crespo had access only to Abrams (1944) as a means of comparison of the Argentinian material with North American species. When J. T. Howell of the California Academy of Sciences called my attention to their paper in 1970, I came to the conclusion, based on their illustration (as well as Buchinger's plate) that *E. ameghinoi* was probably a synonym of *E. divaricatum* Hook. This point was reinforced by Moreau and Crespo's observation that a five-parted involucre was present as Spegazzini (1902) had stated, and not lacking as Johnston had implied.

Eriogonum divaricatum is an annual herb found often on gumbo clay hills and flats in the Colorado and Green river drainage basin of southwestern Wyoming southward

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through eastern Utah and adjacent western Colorado into northwestern New Mexico and northern Arizona (Reveal 1973, 1976). It is also on the northern shore of Sevier Lake, Millard Co., western Utah (Reveal & Reveal 4001). This reduction of *Sanmartinia* and *E. ameghinoi* to *E. divaricatum* was suggested by Reveal and Howell (1976) in the key to genera of the subfamily Eriogonoideae and later repeated in more detail in a review of the subfamily (Reveal 1978); however, in both instances this was done based solely upon observations of illustrations and not the actual examination of the specimens.

Two of the collections of *Eriogonum ameghinoi* (both at LP) have been made available for study (a third is at BA, fide Moreau and Crespo [1969]). These two specimens were *Ameghino 11317* from Lago Colhue-Huapi, Dpto. Sarmiento, Chubut, Argentina, gathered in 1900, and *Ameghino 11318* from between San Julian and Río Deseado, collected in 1899. The first collection, the more mature of the two, and the one on which Spegazzini (1902) based his description, is here selected as the lectotype for the species. The nearly complete specimen in the upper left-hand corner of the lectotype served as the basis for the illustration in both Buchinger (1950) and Moreau and Crespo (1969). This collection was gathered near a large, inland lake located west-northwest of Comodoro Rivadavia in southeastern Chubut. The second collection came from an unknown location somewhere between Río Deseado and San Julian. This is an arid region dotted with occasional lakes, but the distance between the two reference points is nearly 300 km, and it is impossible to determine where the collection was made. The third specimen (not seen by me) was gathered at Deseado, a small town on the Atlantic coast near the mouth of Río Deseado. The last two collections came from eastern Santa Cruz.

In the intervening years *Eriogonum divaricatum* has not been recollected in South America. That it was relatively widespread is shown by the three separate sites where it was collected, a distance of perhaps 400 km north-south. Although it is likely that Ameghino selectively collected sites where the *Eriogonum* might be found, that he found it and no one else has may be due to a series of

unique events that have not been subsequently repeated.

Eriogonum divaricatum occurs in heavy clay soil that tends to clump when wetted. In some years in eastern Utah, great masses of annual *Eriogonum* species will be found in flower. This is particularly true of *E. inflatum* Torr. & Frém. var. *fusiforme* (Small) Reveal, but will occasionally happen in such species as *E. scabrellum* Reveal, *E. subreniforme* S. Wats., *E. wetherillii* Eastw., both species of the genus *Stenogonum* Nutt. (see Reveal and Ertter 1977), and even *E. divaricatum*. Unlike most of these species, *E. divaricatum* is in full fruit during the early fall of the year. By this time the other annuals have dropped their seeds, or, in the case of *E. scabrellum*, will not be in full fruit until late in the fall.

The distribution of *Eriogonum divaricatum* is relatively widespread in the Intermountain West, occurring, as noted above, from Wyoming to New Mexico and Arizona. Within such a large area it would normally be difficult to determine where the South American plants came from were it not for minor populational differences in the floral hair morphology associated with the tepals of *E. divaricatum*. The hairs of the South American plants are long, slender, smooth, and pointed at the tip on mature tepals. The hairs on tepals from plants gathered in northern Arizona, western Utah, and southeastern Utah are short, bulbous apically, smooth, and rounded at the tip. Hairs of other plants gathered in northern Arizona and eastern Utah are similar to those of the South American plants except that the shaft of the hair is slightly papillose and not smooth. An examination of floral hairs from plants gathered in scattered portions of northeastern Arizona most closely resemble the hairs of the South American plant, with those found on an Eastwood and Howell collection (6497-US) gathered near Cameron, Coconino Co., being the most similar.

Because *Eriogonum divaricatum* is common along major waterways in this part of Arizona, and elsewhere in its range, and these waterways are heavily visited by migratory birds, I suspect that the introduction of *E. divaricatum* into portions of Argentina located precisely at the southern end of a

major north-south flyway (see National Geographic Map, "Bird Migration in the Americas," Aug. 1979) was accomplished by migrating birds. It is unlikely that seeds of the *Eriogonum* were eaten but not digested and passed in a viable state. Rather, it is more likely that seeds were attached to birds, probably on mud-caked feathers, and carried passively to South America. Only a few groups of birds have this extended pattern of distribution, and one of them is the shore bird. Of the several species that are found in the Intermountain West, e.g., *Bartramia longicauda* (Upland Plover), *Tringa solitaria cinuamoma* (Western Solitary Sandpiper), and *Totanus flavipes* (Yellow-legs), among others (Bailey 1928, Hayward et al. 1977), only one, *Totanus flavipes*, is common throughout the area where the *Eriogonum* occurs in Argentina (Olrog 1968). Interestingly, this species, as with other shore birds, is capable of flying the entire distance from Utah and Arizona to South America nonstop (J. W. Aldrich, pers. comm.).

Why *Eriogonum divaricatum* has not been recollected in Argentina cannot be determined, but that fact alone should not exclude the possibility that the species is not still extant in the country. If extirpated, however, some consideration can be given to the introduction of *E. divaricatum* into Argentina as a single, unique event. If there was a large population of *E. divaricatum*, say in north-eastern Arizona, that was fed upon at the same time by numerous birds, and by some remarkable event seeds ended up in Argentina in different places, germinated, and grew and plants were fortuitously collected by a botanist during the one growing season that the plants were extant, this would have been astonishing.

It is possible that *Eriogonum divaricatum* persisted in Argentina for several thousands of years. The floral hair differences are admittedly slight but do indicate a slight degree of divergency that could be associated with isolation (see Grant [1967] for an example in *Gilia*). The length of time that that divergency may have had to develop is another matter. As Raven (1963) has pointed out, the timing of the various migration events into South America from North America is still confusing, and, though I feel (Reveal 1978)

the introduction of *E. divaricatum* occurred during the Quaternary, I cannot state for certain when. If the plants persisted for only a few years after their initial introduction, and during one of the growing seasons Ameghino found them and made collections, then the species might never have truly become established. If the species was extirpated naturally after Ameghino collected the plants, the events associated with the extirpation will never be ascertained. If the buckwheat was recently introduced, as a result of a one-chance event, then its extirpation might have been just as sudden.

ACKNOWLEDGMENTS

I thank Dr. Angel L. Cabrera and the staff at the Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, for making the specimens of *Eriogonum ameghinoi* available, and Dr. J. W. Aldrich, Department of Ornithology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., for his help with determining bird species that might be responsible for the distribution of *Eriogonum* in South America. Dr. John L. Strother kindly reviewed and commented upon a draft of the manuscript.

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COMPOSITIONAL SIMILARITY WITHIN THE OAKBRUSH TYPE IN CENTRAL AND NORTHERN UTAH

L. M. Kunzler,¹ K. T. Harper,¹ and D. B. Kunzler¹

ABSTRACT.—Indices of similarity were used to evaluate the similarity of oakbrush stands throughout the Uinta National Forest and to compare oak communities in central and northern Utah. Results show that Gambel oak stands in central Utah differ significantly among themselves in respect to quantitative aspects of the vegetation. Those differences can be correlated with elevation, slope exposure, and fire history. Nevertheless, there is currently inadequate justification for recognizing more than one habitat type for the species in the study area. There is a need to develop a model capable of predicting growth rate of oak on specific sites.

The Gambel oak (*Quercus gambelii* Nutt.) community is an important constituent of big game winter ranges in Utah. Land managers responsible for this vegetation type desire to manage it so as to enhance wildlife habitat, provide maximum forage for big game, and maintain stable soil conditions on watersheds (pers. comm., Juan Spillett, wildlife biologist, Uinta National Forest). To develop a management scheme to meet those objectives, it would be helpful to know how similar oakbrush stands are within the area of concern. Accordingly, oak stands throughout the Uinta National Forest and surrounding areas have been examined for vegetational similarity using both quantitative and qualitative data.

LITERATURE REVIEW

For the most part, current oakbrush literature treats the oakbrush type as if it were uniform at all elevations, exposures, etc. A few studies indicate that there are regional and ecological differences within the Gambel oak type (Dixon 1935, Brown 1958, Cronquist et al. 1972). Those authors suggest that oakbrush is successional to ponderosa pine in southern Utah and Colorado. Allman (1953), Christensen (1958), Nixon et al. (1958), Nixon (1961, 1967), and Eastmond (1968) suggested that the oak zone is successional to maple in central Utah. Christensen (1964) reported that on north-facing slopes in Provo Canyon, Utah, oakbrush was successional to white fir and Douglas-fir. In Colorado, Steinhoff (1978) recognized seven

different oakbrush associations with five successional stages in each. Although those associations tended to be quite similar, they were made distinct from each other by the presence or absence of a major plant indicator species for each of the groups.

METHODS

Quantitative vegetational data were collected in 23 oakbrush stands located throughout the Uinta National Forest and in surrounding areas at different elevations and exposures. Of the 23 stands, 14 had been burned within the last 30 years, with the majority of those having burned within eight years of the sampling date. Nine of the burned stands were paired with adjacent, nonburned stands of approximately the same elevation, exposure, and slope.

Qualitative (species presence) data were also taken in an additional four oakbrush stands situated above 2040 m (6700 ft) and with north to east exposures. Quantitative data were collected from 0.04 ha (0.1 acre) stands using 25 quadrats of 0.25 m² area. Quadrats were uniformly placed across the surface of each stand. Species present in each quadrat were recorded and the foliage cover of each was estimated using the following cover classes: 0, no cover; T, <1.0%; 1, 1–5%; 2, 5–10%; 3, 10–25%; 4, 25–50%; 5, 50–75%; 6, 75–95%; and 7, >95% cover.

Using quantitative data and all possible combinations of the 23 Central Utah stands taken two at a time, a stand matrix was con-

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structed based on Ruzicka's (1958) index of quantitative similarity. A cluster dendograph was drawn to illustrate the results of the Ruzicka interstand similarity matrix. The dendograph was constructed using the unweighted clustering method of Sneath and Sokal (1973). The average internal similarity among stands within each of the groups detected by cluster analysis was computed and each group was tested for significance of difference from other groups using the values for the Ruzicka index and analysis of variance.

In order to determine whether species composition (qualitative data only) differed significantly between unburned and burned stands or between higher elevations (>1830 m or 6000 ft) and lower elevation (<1830 m or 6000 ft) stands, all possible combinations of stands of concern taken two at a time were tested for qualitative similarity using the Jaccard (1912) coefficient of community. To maximize possible vegetational difference between stands, six stands above 2040 m (6700 ft) with north to east exposures were compared with six stands that occurred below 1740 m (5700 ft) and on south and west exposures. The method described by Beers et al. (1966) was used for converting aspect values (degrees) to a form that permits one to statistically test for aspect differences between groups of stands.

To compare the composition of central Utah oak stands with that for northern Utah oak stands, Ream's (1963) prevalent species list was compared with prevalent species lists for our burned and unburned stands taken separately and combined (Table 1). Both qualitative (Jaccard 1912) and quantitative (Ruzicka 1958) similarity indices were used to measure the degree of similarity between prevalent species lists from the central and northern Utah oakbrush zones. We have also evaluated the similarity of the foregoing prevalent species lists to the prevalent species list for northern Utah bigtooth maple stands sampled by Ream (1963).

Prevalent species were determined for all central Utah oak stands combined and for burned and unburned stands separately. Those species were selected using the method of Curtis (1959) as modified by Warner and Harper (1972). Curtis (1959) considered the number of prevalent species for a community

to be equal to the average number of species per stand in that community type. Prevalent species were identified by ranking all species encountered in decreasing order of average quadrat frequency in all stands sampled. Prevalent species were then selected from the top of the list until a number equal to the average number of species per stand was reached.

RESULTS

Gambel oak stands (0.04 ha) in central Utah supported 25 plant species on the average (Table 1). Gambel oak itself was the most commonly encountered species in the study. Of the two next most abundant species, one was introduced (*Bromus tectorum*) and the other was native (*Galium aparine*). Both of the latter-named species were annuals. In total, the list includes six shrub species, six perennial grasses or grasslike species, four annuals, and nine perennial forbs. The most abundant associated shrub was snowberry (*Symphoricarpos oreophilus*); the most common grass was the introduced Kentucky bluegrass (*Poa pratensis*); and the most frequently encountered perennial forb was peavine (*Lathyrus pauciflorus*). There were 4.07 plant species per 0.25 m² quadrat.

When prevalent species were selected on the basis of fire history in oak stands (Table 1, columns 2 and 3), it is apparent that burning encourages annual plant species. The following annuals are over twice as frequent in burned as unburned stands: *Bromus tectorum*, *Collomia linearis*, *Epilobium paniculatum*, and *Lactuca scariola*. In burned stands, annuals contribute over 27 percent of the sum frequency of prevalent species, but in unburned stands, annuals account for only about 13 percent of the sum frequency of prevalents. Other plants that increased strongly with burning were *Artemisia ludoviciana*, *Chrysothamnus viscidiflorus*, and *Lupinus* sp.

In contrast, several species appeared to be severely reduced when oak stands burn. Both lichen (*Cladonia* sp.) and moss (*Polytrichum* sp.) frequently dropped to zero on burned areas. Big sagebrush (*Artemisia tridentata*) and bluebunch wheatgrass (*Agropyron spicatum*) were also seriously handicapped by fire.

TABLE 1. Average frequency of species found on the prevalent species list for different oak community types in Utah.

Species	Type ¹				
	1	2	3	4	5
<i>Quercus gambelii</i>	81.4	82.2	80.8	85.7	52.9
<i>Galium aparine</i>	34.6	36.8	33.1	23.1	49.0
<i>Bromus tectorum</i>	27.8	9.8	39.4	38.6	10.0
<i>Poa pratensis</i>	16.0	16.9	15.4	—	—
<i>Symphoricarpos oreophilus</i>	15.4	22.2	10.9	23.5	8.5
<i>Lathyrus pauciflorus</i>	12.2	10.2	13.4	6.5	13.2
<i>Solidago sparsiflora</i>	11.5	14.2	9.7	—	—
<i>Achillea millefolium</i>	11.2	17.3	7.2	10.5	11.3
<i>Vicia americana</i>	11.1	10.7	11.4	12.1	—
<i>Viguiera multiflora</i>	10.7	° 2.3	16.0	8.8	4.3
<i>Carex hoodii</i>	9.2	8.4	9.7	—	7.1
<i>Amelanchier alnifolia</i>	9.2	16.9	° 4.2	21.0	9.1
<i>Agropyron spicatum</i>	8.7	13.9	° 5.4	11.2	2.8
<i>Prunus virginiana</i>	8.4	12.4	5.7	15.5	33.3
<i>Stellaria jamesiana</i>	7.8	15.1	° 3.1	11.9	12.2
<i>Epilobium paniculatum</i>	7.3	° 3.1	10.0	—	—
<i>Chrysothamnus viscidiflorus</i>	7.2	4.4	8.9	—	—
<i>Agropyron cristatum</i>	7.1	—	11.7	—	—
<i>Hydrophyllum capitatum</i>	6.8	8.9	° 5.4	—	6.3
<i>Rosa woodsii</i>	6.4	7.1	6.0	9.4	3.7
<i>Allium acuminatum</i>	6.4	4.9	7.4	10.9	21.1
<i>Lactuca scariola</i>	6.4	° 1.0	9.8	—	8.5
<i>Aster chilensis</i>	6.1	4.0	7.4	—	—
<i>Agropyron intermedium</i>	5.6	° 0.4	8.9	—	—
<i>Phlox longifolia</i>	5.4	4.4	6.0	5.9	—
<i>Collomia linearis</i>	° 5.3	° 3.6	6.4	10.6	9.8
<i>Elymus glaucus</i>	° 5.2	8.9	° 2.9	—	8.8
<i>Artemisia tridentata</i>	° 5.0	9.6	° 2.1	26.9	12.3
<i>Lupinus</i> sp.	° 4.8	° 2.8	6.1	3.7	4.7
<i>Cladonia</i> sp.	° 4.7	9.8	° 1.4	—	—
<i>Artemisia ludoviciana</i>	° 4.7	° 1.0	7.0	7.2	0.8
<i>Mahonia repens</i>	° 4.6	7.7	° 2.6	10.0	12.8
<i>Balsamorhiza sagittata</i>	° 4.5	° 3.1	° 5.4	11.1	—
<i>Bromus inermis</i>	° 4.4	—	7.1	—	—
<i>Taraxacum officinale</i>	° 4.0	° 1.4	° 5.6	—	1.3
<i>Polytrichum</i> sp.	° 3.7	7.1	° 1.4	—	—
<i>Melica bulbosa</i>	° 3.1	° 1.3	° 4.3	—	3.2
<i>Cirsium undulatum</i>	° 3.1	° 0.9	° 4.6	2.6	—
<i>Collomia grandiflora</i>	° 2.1	° 0.4	° 3.1	6.3	7.5
<i>Tragopogon dubius</i>	° 1.9	° 0.9	° 2.5	1.7	—
<i>Bromus japonicus</i>	° 1.7	° 1.8	° 1.7	—	5.4
<i>Agropyron subsecundum</i>	° 1.7	° 1.3	° 2.0	—	6.7
<i>Acer grandidentatum</i>	° 1.6	° 2.7	° 0.9	7.5	74.3
<i>Crepis occidentalis</i>	° 1.2	° 1.3	—	3.1	3.1
<i>Cynoglossum officinale</i>	° 1.1	° 2.3	° 0.4	—	3.0
<i>Purshia tridentata</i>	° 0.9	° 2.2	° 0.1	4.4	—
<i>Pachistima myrsinites</i>	° 0.7	—	° 1.1	13.0	—
<i>Polygonum douglasii</i>	° 0.7	—	° 1.1	9.4	9.6
<i>Wyethia amplexicaulis</i>	° 0.5	° 1.3	—	7.5	5.2
<i>Senecio integerrimus</i>	° 0.4	° 0.4	° 0.3	3.0	3.4
<i>Xanthocephalum sarothrae</i>	° 0.2	—	° 0.3	5.6	—
<i>Osmorhiza obtusa</i>	—	—	—	—	10.3
<i>Physocarpus malvaceus</i>	—	—	—	—	9.3
Percent Σ Freq. contributed by prevalent species	83.5	91.9	85.2	—	—
Average no. of species/quadrat	4.07	3.99	4.17	4.28	4.45

¹Type 1—23 oak stands in central Utah, including burned and unburned stands

Type 2—9 unburned stands in central Utah.

Type 3—14 burned stands in central Utah.

Type 4—Oak stands of northern Utah (after Ream 1963).

Type 5—Maple stands of northern Utah (after Ream 1963).

°Indicates nonprevalent species for that type.

Data for nonprevalent species unavailable on Ream's (1963) study plots (Types 4 and 5).

The latter two species probably reinvade burned areas quite readily, however. To compensate for losses of fire sensitive species, managers often reseeded perennial grasses into the ashes of burned oak stands. In this study, two grasses (*Agropyron cristatum* and *Bromus inermis*) undoubtedly owe their existence in oak stands to postfire seeding programs.

Our results suggest that few species are lost completely when an oak stand burns in our area. McKell (1950) concluded that northern Utah oak stands recovered quickly after fire: within nine years, grass species had returned to essentially prefire composition and cover. Shrub layer components were scarcely distinguishable from those of unburned stands after 18 years (McKell 1950).

Nevertheless, there is a marked change in Gambel oak stands in the first four years after a wildfire. In an attempt to quantitatively evaluate the compositional changes due to fire and other environmental influences on oak stands, we have clustered the 23 central Utah stands using the Ruzicka (1958) index of

TABLE 2. Comparisons among the four groups of oak stands shown on Figure 1. Groups are compared in respect to fire history, elevation, and exposure. Exposure is transformed using the procedure of Beers et al. (1966).

Characteristics	Group			
	1	2	3	4
No. stands in group	6	7	7	3
Percent of stands that were recently burned	100	29	57	67
Average number of years since last burn ¹	3.5	9.0	9.3	19.0
Average elevation (m)	1,742	1,829	1,837	2,195
Average exposure ²	0.97	1.36	0.65	0.32

¹Only burned stands considered.
²Small values represent southerly exposures; larger values (>1.0) represent northerly exposures.

quantitative similarity and the unweighted mean clustering procedure of Sneath and Sokal (1973). The results (Fig. 1) show four distinct groups of stands that differ among themselves in respect to fire history, elevation, and exposure. The most recently burned stands occurred at lower elevations (Table 2): that pattern is probably a reflection of the frequency with which the average oak stand

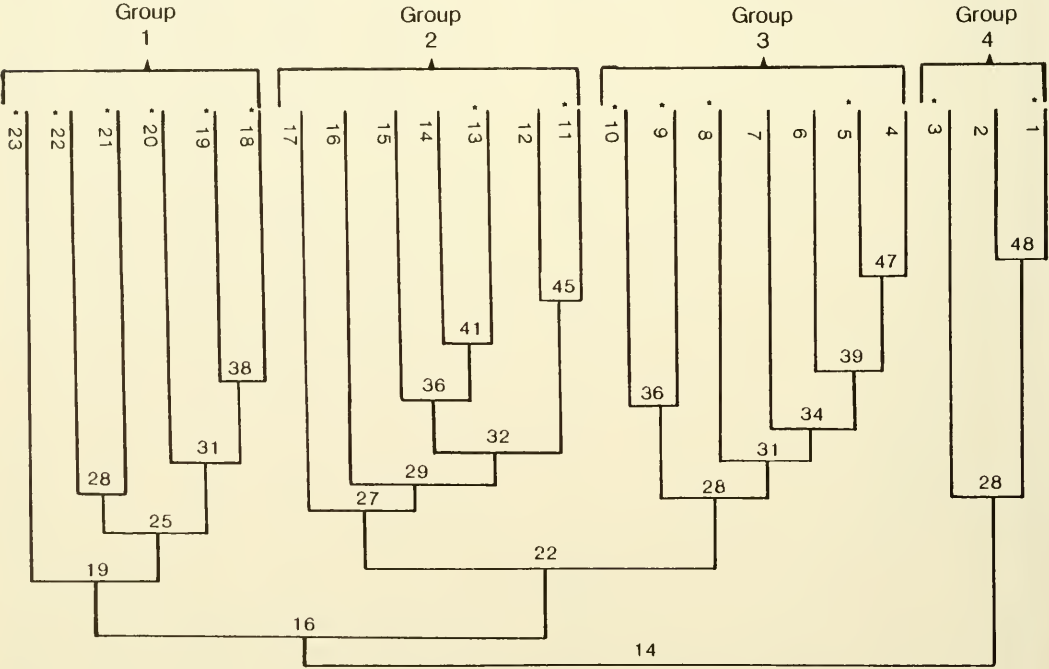


Fig. 1. Similarity dendrogram based on percent similarity values among all possible two-by-two combinations of 23 oakbrush stands from central Utah. The similarity values are based on the Ruzicka (1958) index. Numbers at the branch ends are stand identification numbers. Other numbers at cluster points in the figure report the average similarity value among stands grouped at that level. Recently burned stands are designated by an asterisk by their number. Table 2 should be consulted in connection with this figure.

burns at low and high elevations. Fire history appears to be no more important than elevation and exposure in determining which stands cluster closely and are hence compositionally similar. Low elevations apparently favor some of the same species that increase with burning.

Considering only prevalent species for burned and unburned stands in our central Utah sample (Table 1), Jaccard's index shows those two groups to be over 48 percent similar. However, when both prevalent and non-prevalent species in Table 1 are considered, burned and unburned areas are 86 percent similar. Ruzicka's index of quantitative similarity (using frequency data) show the two lists to be 54 percent similar. These results agree with those of McKell (1950) and Hallisey et al. (1976), who show that, though burning affects the frequency of the species in oakbrush stands, it has few lasting effects on the species composition of those stands.

It is important to note that six high elevation stands on north-facing slopes were more similar to six low elevation stands on south-facing slopes by the Jaccard index (48 percent average similarity) than stands in either group were to each other (45 percent average internal similarity for the high elevation stands and 41 percent similarity among low elevation stands). An analysis of variance showed that between-group similarity differences were not statistically different from within-group differences. T-tests demonstrated that elevation and aspect did differ significantly between these two groups.

Perhaps the most significant aspect of Figure 1 is that within-group similarity is low even among stands of similar fire history. Group 1 is particularly impressive in that respect. Even when stands within groups are compared on the basis of species presence alone (Jaccard's index), within-group similarities are low. Average within-group similarity for groups 2 and 3 was only 57 and 45 percent using the Jaccard (1912) index. Between-group similarity using that index averaged 42 percent for groups 2 and 3 and 40 percent for all possible comparisons among the 23 stands. Thus, while Figure 1 demonstrates that recently burned stands often tend to be more like each other than like unburned or old-burn stands, they differ

markedly among themselves. An analysis of variance test based on stand similarity within and between the groups of Figure 1 shows no statistical significance between groups. There is, thus, too much similarity among the stand groups derived from our sample to justify recognizing more than one Gambel oak habitat-type in central Utah.

How similar are northern Utah Gambel oak stands as sampled by Ream (1963) to those in our sample? We show the frequency of the prevalent species of Ream's (1963) oak samples in Table 1. Since bigtooth maple (*Acer grandidentatum*) is a successional species that displaces Gambel oak on many Utah sites, we also present Ream's (1963) list of prevalent species for the bigtooth maple community (Table 1). It will be noted that Ream recognized more prevalent species and more understory species per quadrat for the Gambel oak type than we show for central Utah (32 versus 25 prevalent species per stand and 4.3 versus 4.1 species per quadrat, respectively). Those differences are probably more a function of sampling methods than vegetational differences, since Ream's (1963) stands were at least three times and his quadrats four times larger than ours. His stands were apparently over 0.1 ha in size and his quadrats had an area of 1.0 m². In contrast, we used 0.04 ha stands and 0.25 m² quadrats.

We have assessed the similarity of Ream's (1963) Gambel oak and bigtooth maple prevalent species lists to the combined prevalent list for our 23 central Utah Gambel oak stands (Table 1). Similarity was determined using both quantitative (Ruzicka 1958) and qualitative indices (Jaccard 1912). The results (Table 3) demonstrate that similarity is always greater between central and northern

TABLE 3. Percent similarity of oak communities of central and northern Utah. Maple communities of northern Utah are also compared to the oak samples. Ruzicka's (1958) and Jaccard's (1912) indices are used for the comparisons.

	N. Utah Oak × C. Utah Oak	N. Utah Maple × C. Utah Oak	N. Utah Maple × N. Utah Oak
	Percent similarity		
Jaccard's	62.7	62.3	55.8
Ruzicka's	48.9	37.3	36.7

Utah prevalent species lists when the comparison is based on species presence alone (i.e., Jaccard's index). Furthermore, the central and northern Utah prevalent species lists are more similar than subgroups of Figure 1 are to each other. Thus, there appears to be no significant differences in composition of oakbrush stands in these two areas.

The central Utah oak community prevalent species list is less similar to the prevalent species list for northern Utah bigtooth maple communities than to the oakbrush prevalent species list for the northern area, but there is still a qualitative similarity of about 63 percent. Nevertheless, even that value is greater than the internal similarity among oak stands shown in Figure 1. It seems apparent that the bigtooth maple community is closely related to the oakbrush type in northern Utah. In all probability, most of the maple stands sampled by Ream (1963) were late seral stages of the oakbrush type.

Although there is inadequate data to support recognition of more than one Gambel oak type in central and northern Utah, there is obvious variation in oakbrush growth rates and terminal size in different ecological situations. There is a need to evaluate and describe site differences that contribute to the marked variations in growth rates of the species in this area. Such information would undoubtedly lead to a subdivision of the oakbrush type into ecological units that would have considerable utility for managers.

CONCLUSIONS

Considerable similarity exists between the prevalent species lists for oak stands in central Utah and prevalent species lists for that vegetational type in northern Utah. The results indicate that for general purposes, at least, one can consider the oakbrush zone of central and northern Utah as one vegetational type. Results further indicate that burning within the oakbrush zone of central Utah has an immediate effect on the ratio of shrub-to-herb forage production and on the ratio of annual-to-perennial herb production. Nonetheless, fire eliminates few, if any, species from oak communities, and burned stands quickly return to prefire species composition. There is a need to develop a model

for predicting growth rates of Gambel oak on specific sites.

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ADDITIONAL DISTRIBUTION RECORDS AND ABUNDANCE OF THREE SPECIES OF SNAKES IN SOUTHWESTERN IDAHO

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ABSTRACT.— New county records are reported for *Hypsiglena torquata* and *Rhinocheilus lecontei*, and additional distribution records are presented for *Sonora semiannulata* in southwestern Idaho. These three species are more abundant than indicated by previous records.

The specific distribution of some of the more secretive snakes in Idaho is poorly known. Erwin (1925) made the first reported collections of the western ground snake, *Sonora semiannulata*, and the night snake, *Hypsiglena torquata*, in Idaho. Later, Tanner (1941) and Slater (1941) each accumulated information on the distribution of amphibians and reptiles in Idaho. Tanner recorded the only known locality of the longnose snake, *Rhinocheilus lecontei*, from Elmore County and listed three localities each for the western ground snake and night snake. Tanner also noted that a specimen of the ground snake was reportedly collected along the Snake River south of Caldwell, Canyon County. Slater (1941) listed the longnose snake only from Elmore County, the ground snake only from Ada County, and the night snake from Canyon and Ada Counties. Medica (1975) recorded the longnose snake from Elmore County and Pendlebury (1976) reported one new record of this snake from Owyhee County. Linder and Fichter (1977) reported five locality records of the longnose snake (Elmore and Owyhee Counties), four localities of the ground snake (Ada, Owyhee, Elmore, and Canyon Counties), and four county records for the night snake (Ada, Bannock, Blaine, and Canyon Counties). Six new records of the western ground snake were published recently by Ralston and Clark (1978). In the following paper, we add further to the knowledge of the distribution and abundance of these three snakes in Idaho.

METHODS AND MATERIALS

The senior author participated in an intensive study of the reptiles of the Birds of Prey Natural Area (BPNA) along the Snake River in southwestern Idaho, from 1975 to 1979. During the early part of this study, he captured snakes by hand while driving roads, walking transects, and turning rocks and debris. Drift fences were also used during the last four summers of this study. Each drift fence consisted of a 30 m section of galvanized metal 51 cm high with two "snake traps" located 7.6 m from each end. The "snake traps" were boxes 1.2 m long, 0.6 m wide, and 0.3 m high constructed out of 2.3 mm ($\frac{1}{8}$ in) hardware cloth. Funnels lead into the trap from each end. A total of 40 drift fences were operated over a four-year span from 1977 to 1980. The drift fences were placed in a variety of habitats and kept in operation from early May through at least the end of July. In addition, snakes were brought to us by various other members of the BPNA research staff.

RESULTS AND DISCUSSION

We collected 14 desert night snakes, *H. t. deserticola*, from Owyhee, Elmore, and Gem Counties in southwestern Idaho (Fig. 1), new county records for this species. The four localities in Owyhee County are 2.5 mi SSW of Swan Falls, 3 mi E of Oreana, 4 mi NNE of Murphy, and 6 mi S of Swan Falls. The three

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localities in Elmore County are 2 mi SE of Black Butte, 5 mi NE of Grandview, and 6 mi NE of Grandview. The site in Gem County is 1.5 mi E of Emmett. *Hypsiglena t. deserticola* were also collected from 11 sites (45 individuals) in Ada County and one site (one individual) in Canyon County.

Nine western longnose snakes (*Rhinocheilus lecontei lecontei*) were taken from four localities in Ada County and one specimen was collected in Canyon County (Fig. 2). These are new county records for this species. The localities in Ada County are 1 mi SE of Swan Falls, 2 mi S of Swan Falls, 3.5 mi SSE of Swan Falls, and 1 mi NW of Swan Falls. The one site in Canyon County is 5 mi S of Melba. We also collected four *R. l. lecontei* from three additional localities in Owyhee County. Three additional specimens were collected by Roger Whitney during the summer of 1971 around residences at the Marsing Job Corps Center.

We collected 35 Great Basin ground snakes (*Sonora semiannulata isozona*) from 22 localities in Canyon, Ada, Elmore, and

Owyhee Counties (Fig. 3). Although none of these collections represent new county records, we have more than doubled the number of localities from which these species had been previously reported in Idaho (Ralston and Clark 1978). *S. s. isozona* were collected from one site in Canyon County, 10 sites in Ada County, 5 sites in Elmore County, and 6 sites in Owyhee County.

Desert night snakes were collected in a variety of habitats, including rocky areas along the canyon rim of the Snake River, at the base of talus slopes, and in shadescale (*Atriplex confertifolia*) and greasewood (*Sarcobatus vermiculatus*) areas away from the Snake River canyon. Western longnose snakes were collected in almost all major habitats in southwestern Idaho. This included areas adjacent to various agricultural lands, rocky and sandy areas, open desert lands, and riparian habitats. Western ground snakes appear to have the most restricted habitat requirements of these three snake species. With only a few exceptions, all ground snakes were collected in or near talus or scree slopes. The

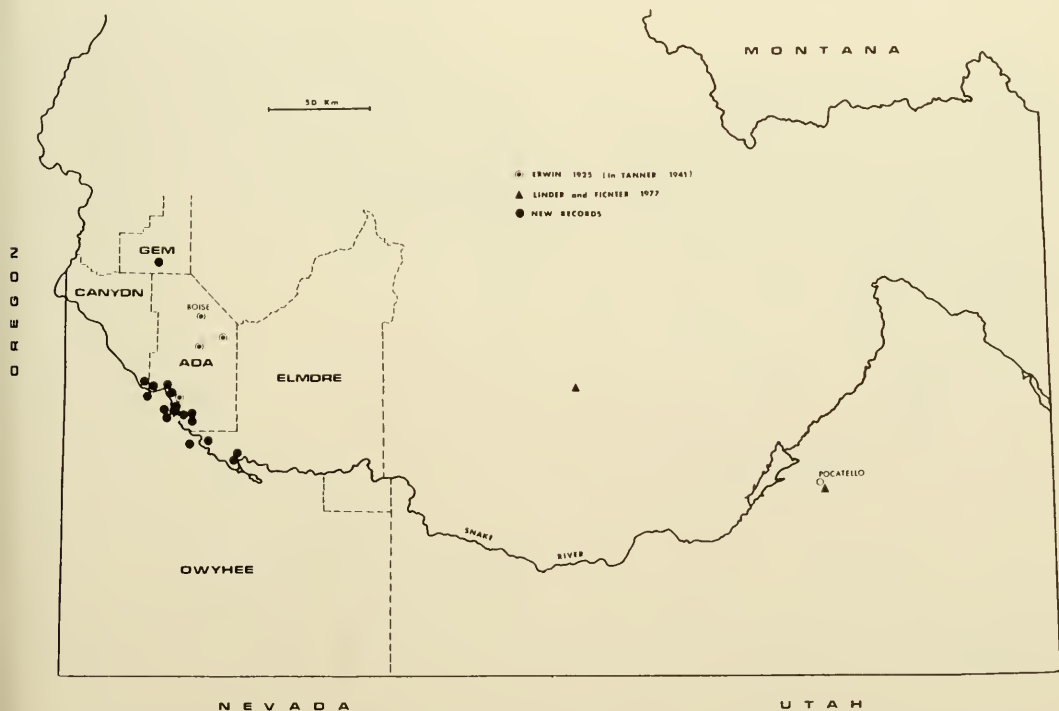


Fig. 1. Distribution of *Hypsiglena torquata deserticola* in Idaho. Some new localities are not shown because of close proximity to other localities.

snakes that were not actually in loose rocky slopes appeared to be utilizing small burrows probably formed by some invertebrate in compact loess near the base of these rocky slopes.

The paucity of records for these three snake species would indicate that they are all rare in Idaho. However, as indicated by Linder and Fichter (1977), they are all secretive, fossorial, or nocturnal snakes that are not easily collected and may be more abundant than the records indicate. Our total collection of 60 night snakes, 46 longnose snakes, and 36 ground snakes confirms that these snakes are not very rare in southwest Idaho and that they can be collected in appreciable numbers by employing the proper techniques. Of the three species, our records suggest that night snakes are the most abundant, followed by longnose snakes, and then ground snakes. Ground snakes seem quite abundant in the areas where they occur, but their more restricted habitat makes their overall abundance low.

Many of the specimens we collected were marked and released for future studies. Most

of the new county records are housed in the reptile collection at the University of Idaho.

ACKNOWLEDGMENTS

We thank Graham Smith and other members of the Snake River Birds of Prey research staff for collecting some of our specimens. Ted Daehnke worked as a field assistant on this study and collected many of the snakes. Roger Whitney provided information on longnose snakes from Marsing. We especially thank Mike Kochert, project leader of the Snake River Birds of Prey research unit, and the Bureau of Land Management for funds that made this work possible.

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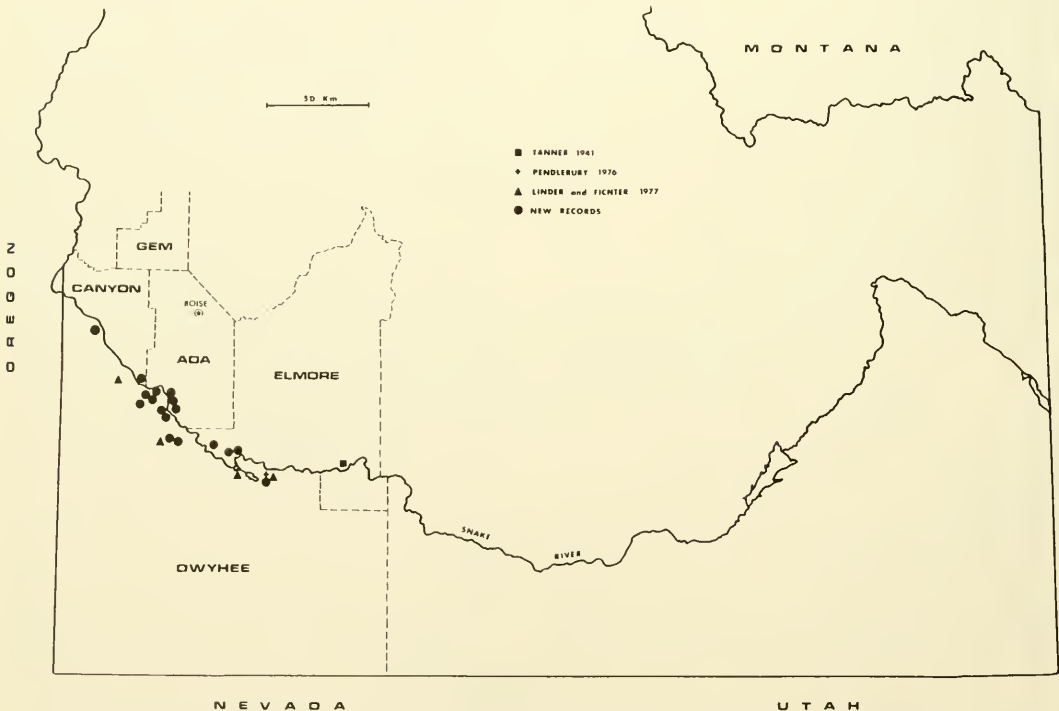


Fig. 2. Distribution of *Rhinocheilus lecontei lecontei* in Idaho. Some new localities are not shown because of close proximity to other localities.

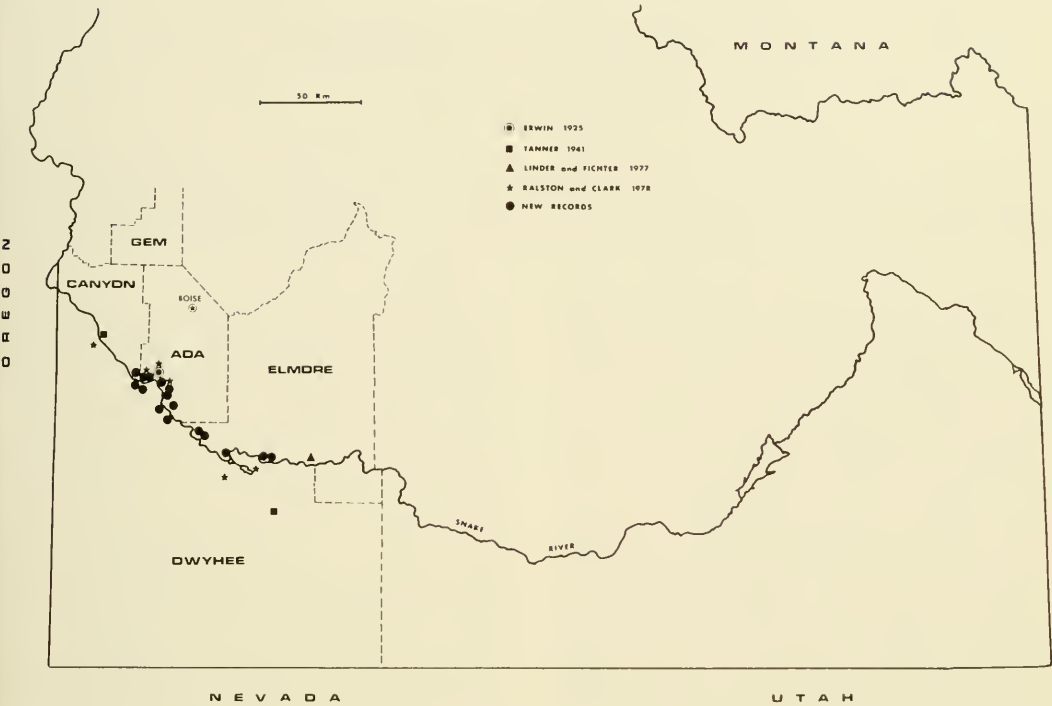


Fig. 3. Distribution of *Sonora semiannulata isozona* in Idaho. Some new localities are not shown because of close proximity to other localities.

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ALARM CALL OF THE PYGMY RABBIT (*BRACHYLAGUS IDAHOENSIS*)¹

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ABSTRACT.— An alarm vocalization was identified in the pygmy rabbit. The call was composed of from one to seven syllables uttered in rapid succession. The syllables were complex tones with many overlying frequencies; the strongest occurred close to harmonic intervals at 4000 and 6000 Hz. In both laboratory and field conditions, the call seemed to be elicited by a potential predator and its use may be unique among leporids.

Squeals or distress calls reportedly were made by several leporids including the brush rabbit (*Sylvilagus bachmani*) (Chapman and Verts 1969), the New England cottontail (*S. transitionalis*) (Olmstead 1970), the desert cottontail (*S. audubonii*) (Orr 1940 and Ingles 1941), and the eastern cottontail (*S. floridanus*) (Marsden and Holler 1964). These calls generally were given by wounded rabbits or in response to human handling. In addition, Marsden and Holler (1964) identified an "alert call" given in response to danger by swamp rabbits (*S. aquaticus*) in a confined population. We describe an alarm vocalization given by the pygmy rabbit (*Brachylagus idahoensis*) (Green and Flinders 1980a).

Alarm signals given by *Lepus* spp. (Kingdom 1974), the European rabbit (*Oryctolagus cuniculus*) (Mykytowycz 1968), and the desert cottontail (Orr 1940) usually were made by thumping the ground with the hind feet. Alarm spread quickly among jackrabbits (*L. californicus*) when one of them sat up with ears erect (Lechleitner 1958). The desert cottontail also used its tail as an alarm signal (Chapman and Willner 1978). When the tail was raised showing maximum white, conspecifics fled to cover.

The pygmy rabbit lacks white flagging on the ventral surface of the tail and may have developed a different strategy to signal alarm. At the U.S. Sheep Experiment Station in southeastern Idaho, these rabbits selected dense brushy habitat (Green and Flinders 1980b), where visual signals of alarm would not be as functional as a vocalization.

Alarm calls given by three caged pygmy rabbits as they were frightened into their den box were recorded at 19 cm/sec (range 40–20,000 Hz) with a Uher 4000-L tape recorder and a Uher M 517 microphone mounted in a 60-cm-diameter parabolic reflector. Recordings were analyzed with a Uher 4000-L recorder and a Kay 6061B Sona-graph Spectrum Analyzer (range 85–16,000 Hz) with a narrow band (20Hz) filter. (Mention of a trade name, proprietary product, or specific equipment does not constitute a guarantee or warranty by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products that may be suitable.)

Seven recorded alarm vocalizations, three single, and four double syllables (two with squeaks) from an adult male rabbit were analyzed. All syllables were similar; the strongest fundamental frequency was about 1350 Hz and lasted about 0.1 sec (range 0.09–0.12 sec). The mean elapsed time between the double syllables was 0.32 sec (range 0.28–0.39 sec). The syllables were complex tones with many overlying frequencies; the strongest occurred close to harmonic intervals at 4000 and 6000 Hz (Fig. 1) and extended above the 16,000 Hz limit of the sonagraph. The vocal pattern of each syllable differed but often contained a rapid rise and fall, producing a "blip." The squeaks at the end of two double-syllable calls were of short duration (0.04 sec) at a frequency of about 1460 Hz. Elapsed time between final syllables and squeaks was 0.90 sec each.

¹This study was supported by USDA Western Regional Federal Cooperative Agreement 12-14-5001-264.

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The alarm call was composed of from one to seven syllables (usually one or two) uttered in rapid succession often followed by one to several squeaks. It was heard numerous times in natural habitat of pygmy rabbits during all seasons of the year. Generally, the call was given by a rabbit as it retreated into a burrow. Calling often continued for several seconds within the burrow and could be heard by an observer 15 m away. Rabbits that waited until they were in burrows to vocalize would be less vulnerable to common predators in the area, coyotes (*Canis latrans*) and red fox (*Vulpes vulpes*), but would increase their inclusive fitness (Dunford 1977). One rabbit gave the call while it stood in an erect, alert position near a burrow entrance; when approached by an observer, it entered the burrow and gave the call again. Another, confined in a live trap, called repeatedly as an observer approached.

Janson (1946:75) noted: "Like other rabbits, the pygmy has a loud quavering squeal when captured. In addition, he sometimes utters a call somewhat resembling that of a pika, but much fainter. When pursued

closely, it often utters a faint squeak of fright." Wilde (1978) also noted the first two of these calls. The distress cry of pygmy rabbits (the loud quavering squeal described by Janson, 1946) occurred when they were removed from wire traps and particularly when they were snared (Green and Flinders 1979). We presume that the "squeak of fright" (Janson 1946) may be a faint distress cry or a part of the alarm call. Rabbits occasionally squeaked after they entered a burrow or den box, but the behavioral significance of this is unknown. The pikalike call (Janson 1946) we assume to be the alarm call similar to the alert call described by Marsden and Holler (1964) for confined swamp rabbits.

In cages, both male and female pygmy rabbits frequently gave alarm vocalizations. Males were perhaps more vocal than females, and certain males regularly emitted the alarm call as they dashed to their den box. In both laboratory and field conditions, the call seemed to be elicited by a potential predator. Alarm calls given by marmots (*Marmota caligata*) (Taulman 1977), ground squirrels (*Spermophilus tereticaudus*) (Dunford 1977),

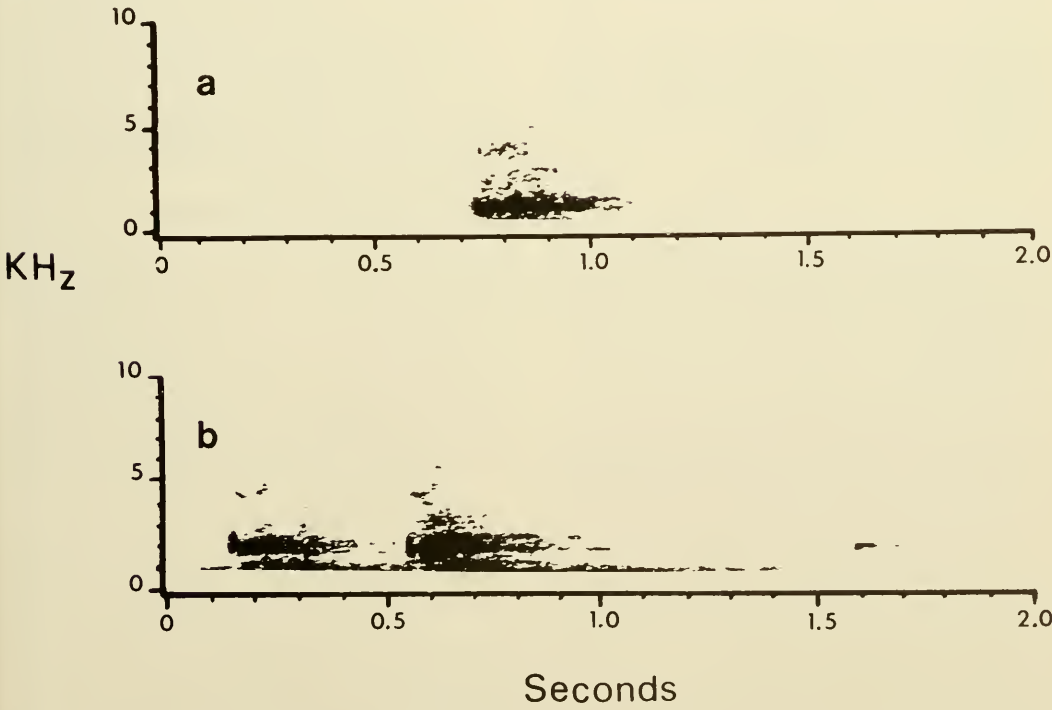


Fig. 1. Sonagraph of a postulated alarm vocalization from the pygmy rabbit: (a) single syllable and (b) double syllable ending with a squeak.

prairie dogs (*Cynomys ludovicianus*) (Smith et al. 1977), and pikas (*Ochotona princeps*) (Lutton 1975) were elicited in similar situations (also see Harvey and Greenwood 1978).

A low chucklelike call occasionally was emitted when a pygmy rabbit was touched while in a trap or cage. A hand-raised female pygmy rabbit emitted the chuckle when disturbed in her box. The chuckle seemed to be a protest to the violation of individual distance and may have corresponded to the grunt in *Lepus* (Lechleitner 1958). Some pygmy rabbits emitted soft barks while entering or leaving their den boxes when there was no discernible cause for alarm.

To our knowledge, alarm calling in leporids under natural conditions has not been reported. The adaptive advantages of giving alarm calls would be greatest in social settings where the likelihood of closely related individuals responding by flight would be increased (Dunford 1977). Pygmy rabbits are associated with sagebrush (*Artemisia* spp.) habitat (Orr 1940) and are generally aggregated (Green and Flinders 1980b). Janson (1946) reported estimates of density for pygmy rabbits based on burrow counts of 0.7 and flush transects of 1.4 rabbits per ha. We found densities of 45 rabbits per ha. It is reasonable to conclude that alarm calls could be selected for this aggregated species living in a habitat with poor visibility.

ACKNOWLEDGMENT

The assistance of D. E. Miller, Washington State University, who provided the Sonagraph Spectrum Analyzer is gratefully acknowledged.

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ULTRASTRUCTURE OF EOCENE FOSSIL PLANTS

E. M. V. Nambudiri,¹ W. D. Tidwell,² and W. M. Hess²

ABSTRACT.— Petrified leaf and pericarpic tissues from the Eocene Deccan Intertrappean beds of India were studied using light and transmission electron microscopy. Degradated cytoplasm with organellelike bodies are present in cells of the leaf tissues. TEM of these cells revealed wall structure and cytoplasmic residues. Microfibril distribution of pericarpic cells resembles fiber cells in extant angiosperms.

Scanning and transmission electron microscopes are widely used in studying fossil plant material. Chaloner and Collinson (1975) demonstrated that additional information on impression fossils could be obtained by using SEM. Grierson (1976), Hartman (1977), and others have studied SEM structures of the vascular tissues of Devonian plant fossils. Several workers, notably Kedves (1974), Pettit (1966), Taylor (1968, 1973a, 1973b), Taylor and Millay (1969, 1977a), and others have reviewed the usefulness of scanning and transmission electron microscopy in paleopalynological investigations.

It was Wesley and Kuyper (1951) who, for the first time, demonstrated that TEM could be used in studying the vascular tissues of *Lepidodendron*. Since then, Eicke (1954), Fry (1954), and Schmid (1967) have employed TEM in studying vascular tissues of fossil plants.

Crepet et al. (1975) and Dilcher (1974) extended the electron microscopy studies to fossil angiospermic leaves and inflorescences. Niklas et al. (1978) described TEM structures of Miocene angiospermic leaves resembling *Zelkova* from the Succor Creek Formation of Oregon. Apart from these, the authors are unaware of any other TEM studies on petrified angiospermic tissues. Therefore, two different plant tissues from the Eocene Deccan Intertrappean series of India were processed for ultrastructural studies. These Intertrappean beds contain some of the best preserved petrifications from India, and until now no electron microscope studies of the

Deccan fossils have been attempted. Hence, the present work forms a unique attempt at describing the ultrastructure of these fossil plant tissues.

MATERIAL AND METHODS

The petrified fossil tissues are embedded in black cherts. Peel transfers of these fossil tissues were cut into 1–2 mm pieces. They were then placed in 1 percent OsO_4 for four to six hours. The sample pieces were transferred from OsO_4 and embedded in agar (2 percent/ H_2O), to prevent disintegration in embedding solvents. The material was then allowed to remain in Uranyl acetate overnight. After dehydration by processing through a series of ETOH and acetone concentrations, the material was embedded in Mollenhauer's resin (1964). Ultrathin sections were subsequently prepared.

RESULTS AND DISCUSSIONS

Leaf Tissues

Several well-preserved petrified leaf tissues were embedded in a black chert. Epidermal cells of the leaf tissue are rectangular (Fig. 2) and many of these cells contain cytoplasm and organellelike bodies (Figs. 2 to 4) representing various degrees of disintegration. From their consistent peripheral orientation, the round to oval organellelike structures (Fig. 2) are similar to the distribution of chloroplasts in extant angiospermic leaves. A

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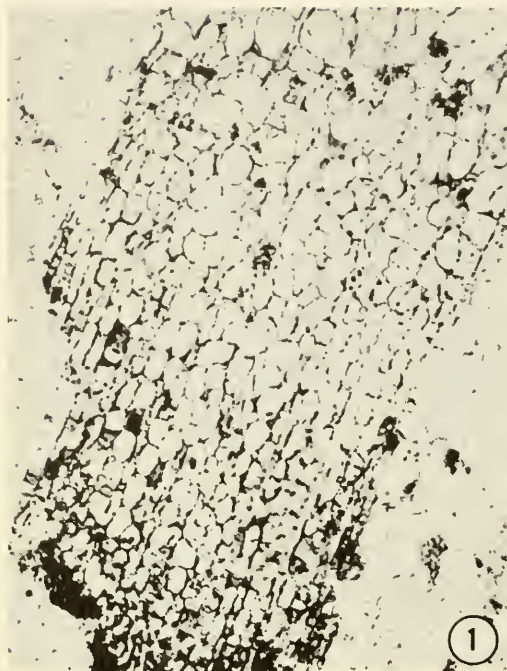


Fig. 1. Light micrograph of the epidermal cells of the fossil leaf tissue, 50X.

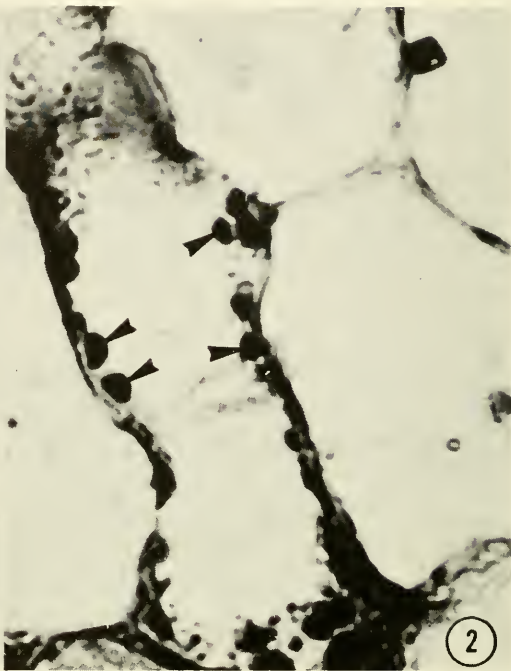


Fig. 2. One of the epidermal cells from the petrified leaf tissue enlarged (light micrograph). Arrows point out the round to oval organellelike bodies, 850X.



Fig. 3. A single cell of the Eocene leaf tissue, demonstrating its internal structure (light micrograph), 750X.

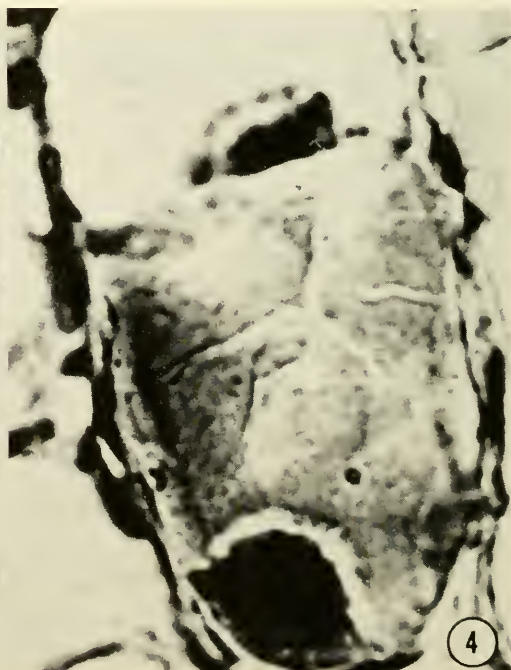


Fig. 4. Cell of the fossil leaf, showing degraded cytoplasm (light micrograph), 1300X.

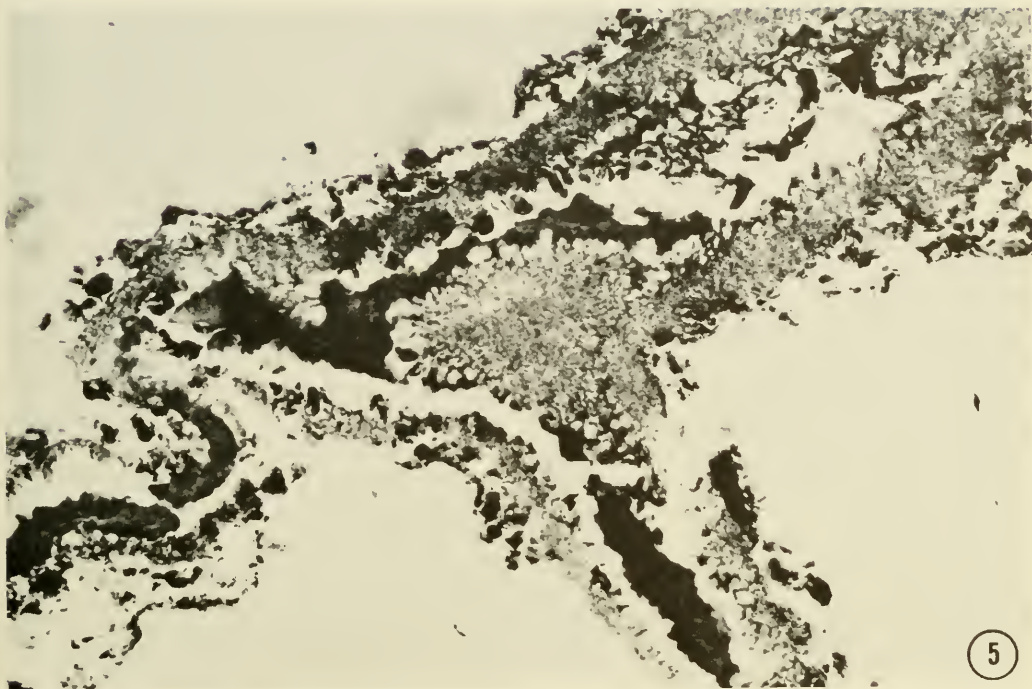


Fig. 5. Structure of cell wall: middle lamella, isotropic layer, and secondary wall are visible (electron micrograph), 13,000X.

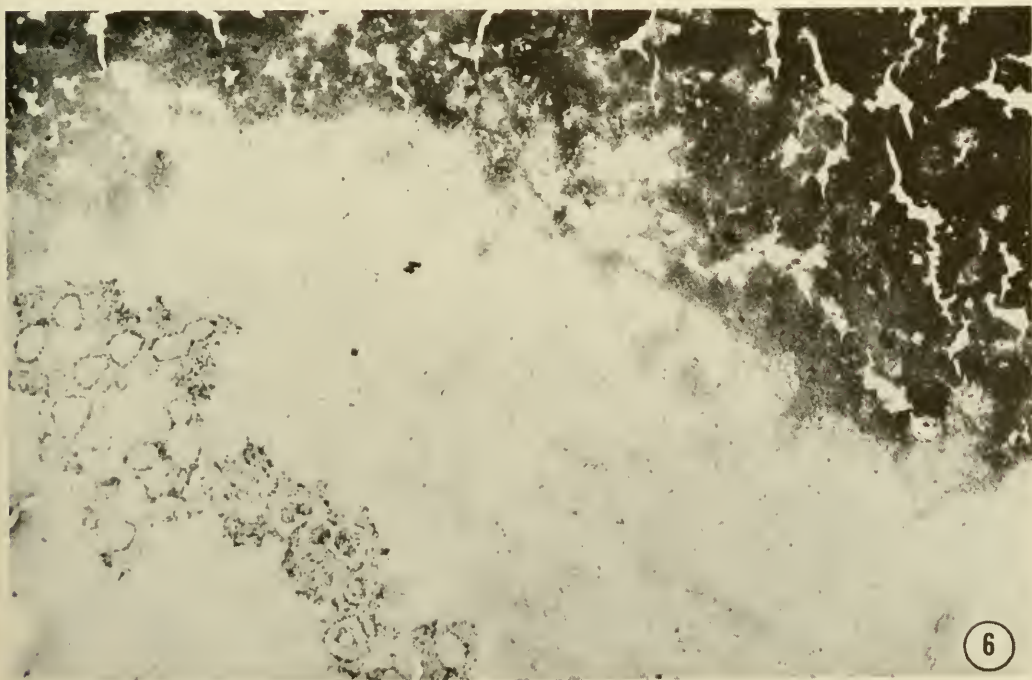


Fig. 6. Cytoplasmic residues inside the cells of the fossil leaf tissue (electron micrograph), 28,800X.

region thought to represent cytoplasm (Figs. 3 to 4) has undergone considerable degradation (Fig. 4), and whether a nucleus is preserved or not is a matter of conjecture.

The presence of protoplasmic material in fossil plant tissues is well documented by several workers. Taylor and Millay (1977a) suggested that cytoplasm and nuclei could be preserved in the microspores of the Pennsylvanian cone genus, *Lasiostrobus*. They later showed evidence for well-preserved cytoplasmic material in *Biscalitheca* spores (Taylor and Millay 1977b). In *Lepidostrobus schopfii* (Brack-Hanes and Vaughn, 1978) and *Zelkova* (Niklas et al. 1978), nuclear material and cytoplasmic residues have been reported. Chlorophyll derivatives were recovered from the Eocene formations of East Germany (Dilcher et al. 1970) and Miocene *Zelkova* leaves (Niklas and Giannasi, 1977). Baxter (1964) reported starch grains in Pennsylvania fossil gametophytes. The presence of protoplasts, although somewhat degraded, in the petrified leaf remains from the Deccan Intertrappean beds, therefore, adds another example of the preservation of cytoplasm and organellelike bodies in plant fossils. Relatively low degradation and, thus, the preservation of cytoplasm and organellelike bodies may have resulted from a rapid deposition in the numerous lakes that occupied the Deccan region in the Eocene period.

Cells of the leaf tissues, on the other hand, retain a wall structure (Fig. 5) that resembles parenchymatous cells in extant angiosperms. Two electron-dense layers are apparent with an isotropic layer between them. At the center, where cell walls meet, the middle lamella attains maximum thickness. The middle lamella is an electron dense layer, and represents a compound middle lamella as in the fossil genus, *Callixylon* (Schmid 1967). Several extant angiosperms such as species of *Populus* (Chafé and Chauret 1974) have similar middle lamellae. The inner electron dense layer corresponds to the inner secondary wall. Thickness of the isotropic layer (Fig. 5) is, perhaps, exaggerated by shearing of the material. S1, S2, and S3 layers, as found in lignified tissues (Schmid 1967), are indistinguishable in this fossil material. Cytoplasm has undergone considerable degradation. Cytoplasmic residues are found adjacent

to the cell walls (Fig. 6). An electron-dense organic matter is occasionally present in the cytoplasmic residue (Fig. 7). The electron-dense nature of this material is perhaps due to the unsaturated bonds that have reacted with the osmic acid and probably is not from the coalification process. These are evidently not artifacts, but may or may not represent part of the cytoplasm.

Pericarpic Tissues

The pericarpic tissues processed for TEM studies are from peel transfers of *Viracarpon* Sahni, a monocot fruit of Pandanaceous affinities (Nambudiri and Tidwell 1978). The mesocarp of the phallanges in *Viracarpon* is formed of thick walled parenchymatous and fibrous tissues. The parenchymatous cells are moderately thick walled and isodiametric. The sclereids, on the other hand, are highly thick walled brachysclereids. The electron micrographs (Figs. 8 and 9) are of structures similar to the secondary wall layers of fiber cells. The microfibril distribution in the pericarpic cells (Fig. 9) suggests similarities with the gelatinous fibers of many extant plants such as *Celtis* sp., *Acer saccharum* and *Populus* sp. (Côté and Day, 1962). These authors observed a gelatinous layer around the secondary walls. The longitudinal splits that traverse the secondary walls (Fig. 2) could correspond to the terminal lamellae reported for the tension wood fibers in *Populus* (Côté and Day 1962).

From this brief TEM study of the leaf and pericarpic tissues from the Deccan Intertrappean beds of India, it is evident that the application of electron microscopy to supplement the anatomical data would further enhance closer comparisons with extant genera of angiosperms.

ACKNOWLEDGMENTS

The authors are grateful to Drs. Karl J. Niklas, Cornell University, Ithaca, New York, and David L. Dilcher, Indiana University, Bloomington, Indiana, for helpful suggestions. For technical assistance we thank Mrs. Connie Swensen.

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Fig. 7. Electron dense carbonaceous matter inside the cells of the fossil leaf tissue (electron micrograph), 13,000X.

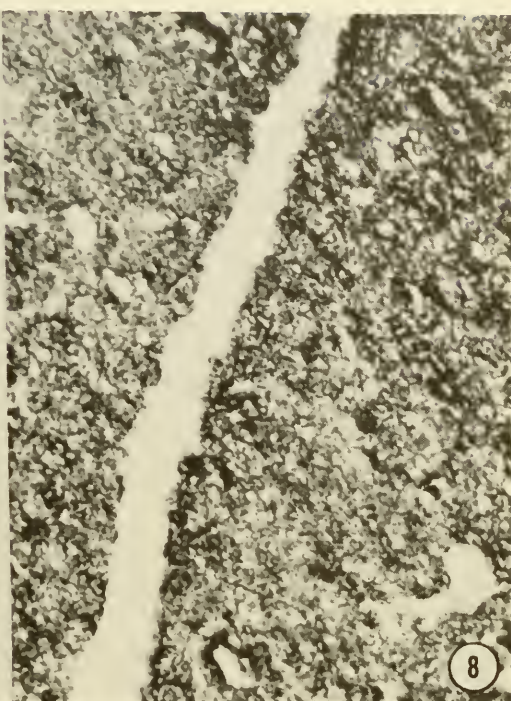


Fig. 8. Pericarpic tissue of *Viracarpou*, illustrating the lamella (electron micrograph), 28,800X.

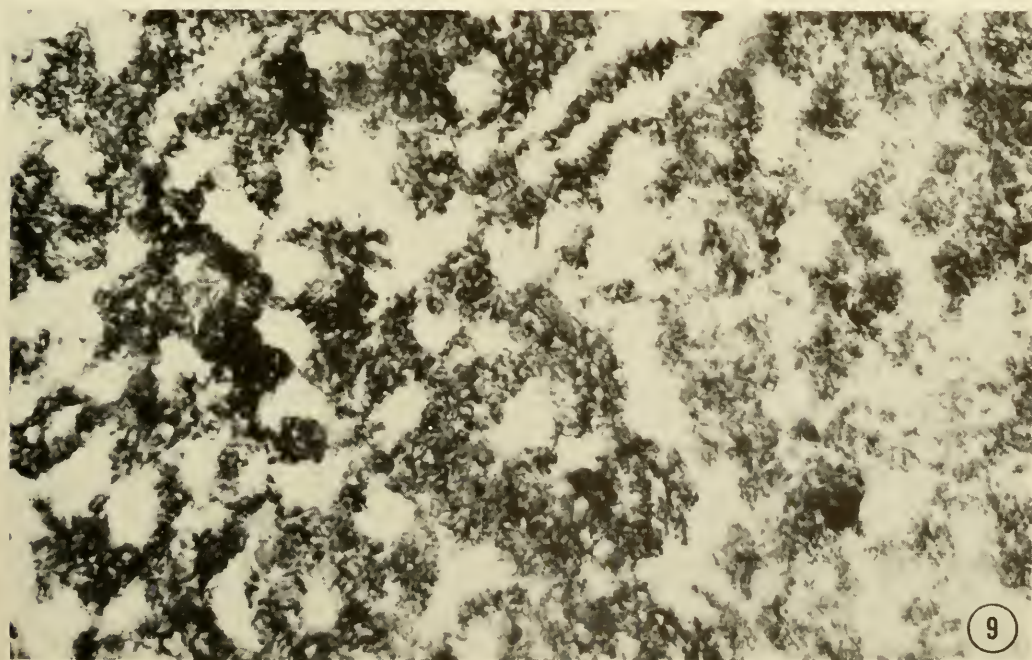


Fig. 9. Electron micrograph of pericarpic cells of *Viracarpou*, showing microfibril distribution, 28,800X.

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THE GREAT BASIN NATURALIST

Volume 41 No. 2

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The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 41

June 30, 1981

No. 2

DISPERSAL AND DISPERSION OF AN INTRODUCED POPULATION OF *SYLVILAGUS FLORIDANUS*

B. J. Verts¹ and Leslie N. Carraway¹

ABSTRACT.— Eastern cottontail rabbits, *Sylvilagus floridanus*, introduced into Linn County, Oregon, in 1941, occupied 378.1 km² in 1953, 637.7 km² in 1970, and 1501.9 km² in 1980. Hiatuses within the range were related to absence of adequate coverts on conifer-dominated ridge tops and in intensively cultivated areas. Flooding of riparian zones seven times during the first 12 years after introduction and three times during the 17-year interval between the first and second surveys (especially the devastating floods of December 1964 and January 1965) was believed to have retarded dispersal or periodically reduced the area occupied. Flood-control dams constructed between 1941 and 1968 on drainage systems that affect the area limited floods to two winters since 1965 and were believed responsible for cottontails extending their range within the county nearly two and one-half fold since 1970. The absence of burrow-constructing associated species was believed relatively insignificant in retarding dispersal. Removal of brushy coverts, particularly by agricultural practices, tended to increase the size of unoccupied areas within the 1970 range of the species.

Eastern cottontail rabbits (*Sylvilagus floridanus*, indigenous to most of the United States east of the Rocky Mountains (Hall and Kelson 1959) were introduced into Linn County, Oregon, near the community of Oakville in May 1941 (Graf 1955). Graf (1955) documented the unsanctioned introduction, reported on a survey of cottontail distribution in Linn County in 1953, and speculated on avenues they used for dispersal. Although the late Professor Graf did not publish his range map in the original article, he gave the map to Verts, who, with a student, repeated the survey of distribution in 1970 and published both maps with suggestions for possible mechanisms of expansion and contraction of the cottontail range during the 17 intervening years (Verts et al. 1972). We wished to reexamine the dispersion of cottontails after 10 additional years and to evaluate the vegetation at all

sites at which cottontails were observed during earlier surveys to ascertain the effect of alterations on current distribution. Also, we wished to evaluate avenues for dispersal, or lack thereof, on distribution of cottontails.

STUDY AREA

Linn County, Oregon, is roughly rectangular (59 x 114 km) and lies near the center of the Willamette Valley (44°12'–44°47'N, 121°48'–123°15'W). It is bounded by the Willamette River on the west, North Santiam River on the north, and the crest of the Cascade Range on the east; the southern border, although largely irregular, is artificial. Elevations range from about 60 m above mean sea level at the confluence of the Willamette and Santiam rivers to nearly 3200 m at the summit of Mt. Jefferson in the Cascade Range; eastward from the Willamette River, relief is

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negligible to the foothills of the Cascades (about 35 km) except for a few scattered buttes near the foothills.

The portion of Linn County in the Willamette Valley is largely agricultural, with production of grass seed (mostly rye grasses, *Lolium perenne* and *L. multiflorum*), wheat, and vegetable crops predominant. Oregon white oak (*Quercus garryana*), Oregon ash (*Fraxinus latifolia*), Douglas fir (*Pseudotsuga menziesii*), and black cottonwood (*Populus trichocarpa*) are typical trees of the riparian zone along major streams. Brambles, particularly blackberries (*Rubus discolor* and *R. laciniatus*), are common along small streams, edges of woodlots, railroad rights-of-way, fencerows, and field borders. Scattered buttes and low foothills are vegetated mostly by deciduous trees, especially oaks, but ridge tops and the west slope of the Cascade Range are covered mostly by subclimax Douglas fir (Johannessen et al. 1970, Franklin and Dyrness 1969).

The climate of the Willamette Valley is moderate; at Corvallis (at the west edge of the study area) January temperatures average 3.8 C, whereas July temperatures average 18.8 C. Precipitation averages 100.8 cm annually, with 82 percent falling between November and May (U.S. Department of Commerce 1978). Temperatures decline and precipitation increases (and the proportion falling as snow increases) with increasing elevation in the Cascade Range.

METHODS

Initially, to establish the current range of cottontails, we traversed all roads in western Linn County surveyed by Graf (1955) or Verts et al. (1972). We made 14 automobile trips from 1 to 18 July 1980 totaling 1390.5 km between 1900 and 2200 h Pacific Daylight Time (PDT). Roads traversed and cottontails observed during each trip were recorded on separate county road maps.

To determine the location and extent of vegetative changes affecting current dispersion of cottontails, we classified all sites at which cottontails were observed during 1953 and 1970 surveys as occupiable or unoccupiable coverts on the basis of the physiognomy of vegetative communities where

we saw cottontails in 1980. Because established populations of cottontails in Oregon seem to require an interspersed of grassy and brushy vegetation, similar to that described for the species in its native range (Schwartz and Schwartz 1959, Atzenhofer and Leedy 1947), we defined an unoccupiable site as one without brushy vegetation within 200 m. This analysis required six trips (20–27 July 1980 between 0430 h and 0745 h PDT) totaling 621.1 km; we recorded roads traversed and cottontails observed as before.

On the basis of the physiognomy of vegetative communities at sites occupied by cottontails, we extended our survey to similar roadside communities from the eastern limit of the 1970 cottontail range to the foothills of the Cascades. From 28 July to 3 August 1980, we made seven trips totaling 1035.6 km between 0445 and 0815 h PDT. We limited our survey at the foothills because we saw no cottontails in coniferous forests and such areas did not support the requisite grassy and brushy vegetation.

We considered the range occupied by cottontails as that area east of the Willamette River that extended 0.8 km beyond the furthestmost points at which cottontails were seen, the same criterion used by Verts et al. (1972). Areas of ranges were estimated by use of a compensating polar planimeter.

RESULTS

In 1980, 96 eastern cottontail rabbits were seen in an area of about 1501.9 km²; thus, the range of the cottontail in Linn County increased nearly two and one-half fold from the estimated 637.7 km² in 1970, which, in turn, was about 40.7 percent larger than the 378.1 km² estimated for 1953 (Fig. 1). However, cottontails were not observed in all areas searched; relatively large areas in the vicinity of Scio, Sweet Home, and Harrisburg seemingly did not contain rabbits (Fig. 1). Also, within the region seemingly invaded within the last decade, distribution was not uniform, and, within the 1970 range, unoccupied areas that were occupied formerly (Verts et al. 1972) continued to increase in size. Nevertheless, approximately three times as many cottontails were observed per 100 km traveled within the 1970 range as in the area

searched in 1970 but in which no cottontails were seen (Table 1).

We judged that only 61 of 111 sites at which cottontails were observed in 1953 by Graf (Verts et al. 1972) supported coverts

occupiable by cottontails, whereas 40 of 48 sites at which cottontails were seen in 1970 were judged to continue to support occupiable vegetative communities (Fig. 2). Current differences in numbers of occupiable

TABLE 1. Distances traveled, cottontails seen, and cottontails seen per 100 km traveled within and outside the 1970 cottontail range in Linn County, Oregon, 1 July–3 August 1980.

Area	Distance traveled		Cottontails seen		Cottontails/100 km	
	Morning	Evening	Morning	Evening	Morning	Evening
Within 1970 range	460.9	820.9	41	18	8.9	2.2
Outside 1970 range	1195.8	569.6	33	4	2.8	0.7



Fig. 1. Distribution of 96 eastern cottontail rabbits observed during roadside surveys conducted 1 July–3 August 1980 and ranges of cottontails in western Linn County, Oregon, in 1953, 1970, and 1980. Roads within stippled areas were searched but no cottontails were observed. Inset depicts location of study area in Oregon. Ranges of cottontails in 1953 and 1970 after Verts et al. (1972).

and unoccupiable sites between the two earlier surveys were significantly different ($X^2 = 11.624$, $df = 1$, $P < 0.01$).

Most cottontails observed in the area seemingly invaded since 1970 occurred in close proximity to water courses (Fig. 3); large hiatuses in the newly occupied range occurred primarily in areas without drainage by permanent streams.

DISCUSSION

Changes in the Range

In the 12 years between introduction and the first survey in 1953, cottontails extended their range about 25 km southward but only about 6 km eastward (Graf 1955). The continuity of suitable coverts along north-south

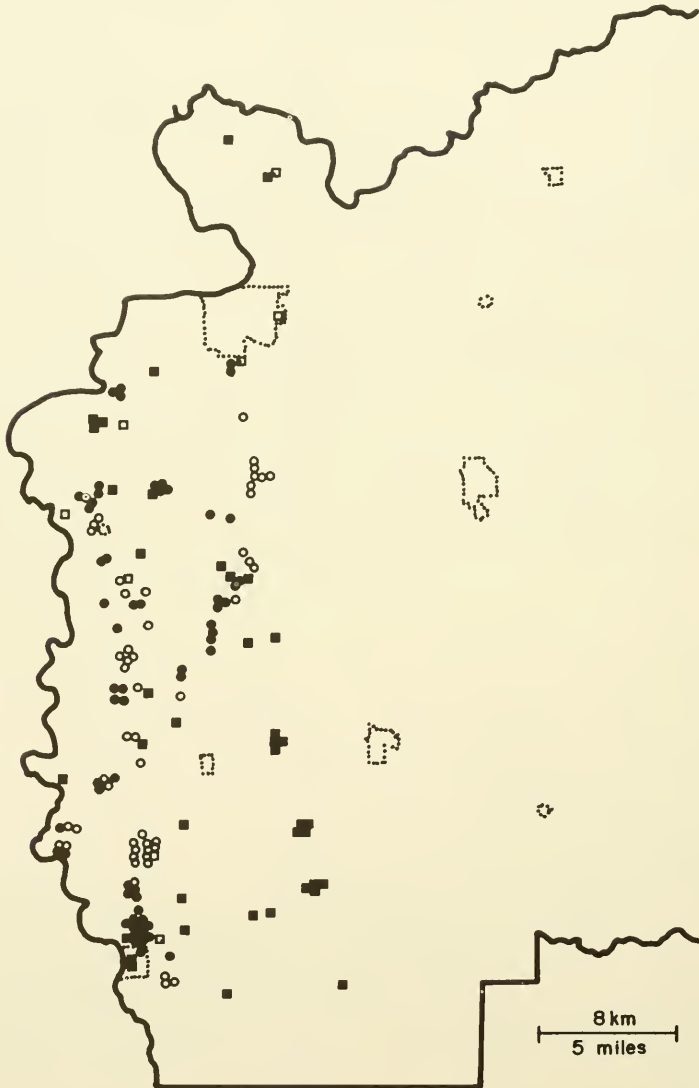


Fig. 2. Sites at which eastern cottontail rabbits were observed in western Linn County, Oregon, in 1953 (circles) and 1970 (squares) (after Verts et al. 1972). Open symbols indicate sites at which no brushy vegetation occurred within 200 m in 1980, thus were judged to be unoccupiable by cottontails.

railroad rights-of-way and the paucity of similar continuous suitable cover eastward from the point of release were offered as possible explanations for directional differences in range expansion (Graf 1955). Destruction of coverts as a result of agricultural practices and winter flooding of riparian zones were offered as explanations for cottontails failing to extend their range to areas beyond the limits of the 1970 range during the 17 years between the first and second surveys (Verts et al. 1972). Because the rate of occupation of new range during the first 29 years after introduction was comparatively modest, the

relatively rapid two and one-half fold expansion in range during the last decade requires explanation.

We cannot discount entirely the possibility that cottontails actually occupied much larger ranges in 1953 and 1970 than described (Verts et al. 1972), and that the rapid increase in range expansion in the last decade was an artifact of survey methods used earlier. However, the three-fold greater numbers of cottontails seen during the 1980 survey in the area occupied by cottontails before 1970 than in the area seemingly invaded during the last decade (Table 1) and the large

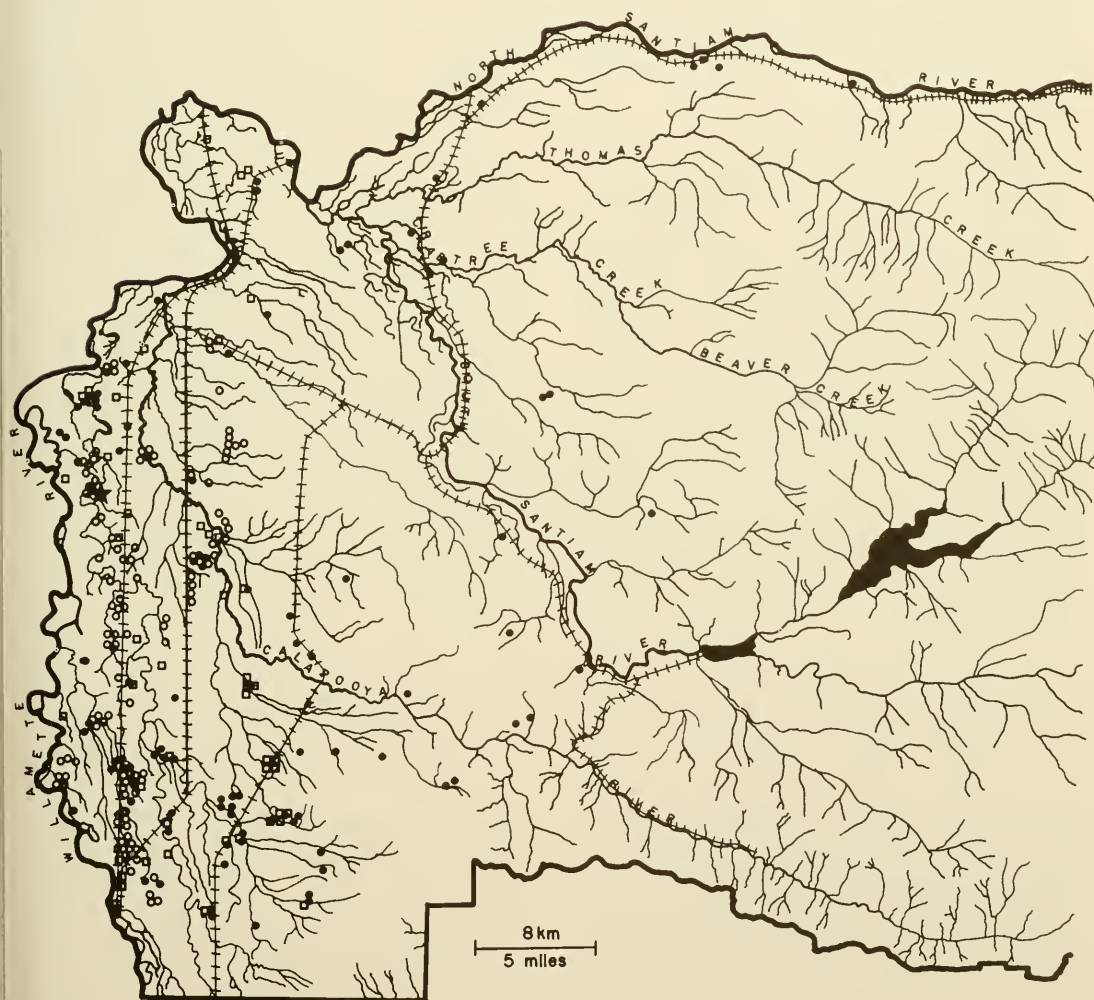


Fig. 3. Distribution of eastern cottontail rabbits observed during roadside surveys conducted in western Linn County, Oregon, in 1953 (open circles), 1970 (open squares), and 1980 (solid circles) in relation to water courses and railroad rights-of-way. Data for 1953 and 1970 from Verts et al. (1972).

hiatuses in distribution within the range occupied since 1970 (Fig. 1) indicate that invasion east of the 1970 range was likely of relatively recent occurrence.

The proximity of sightings of cottontails to streams in areas recently occupied (Fig. 3) indicates that coverts in riparian zones likely were important avenues for cottontail dispersal. Also, in newly invaded range, the relative infrequency that cottontails were seen in areas remote from permanent streams suggests that upland coverts were occupied more slowly than riparian zones. Therefore, we suspect that winter flooding of riparian areas had a significant deleterious impact on cottontail dispersal, and that the frequency and magnitude of floods was responsible for differences in observed rates that new range was invaded.

Since introduction of cottontails, winter flooding was reduced significantly by 10 flood-control dams constructed between 1941 and 1968 (International Commission on Large Dams 1973) on streams or tributaries to streams that drain the study area (Fig. 4). In the 12-year interval between introduction of cottontails and the first survey of distribution in 1953, flooding of riparian zones occurred seven times, possibly explaining the relatively limited dispersal of cottontails during that period (Graf 1955). Although riparian zones were flooded only three times during the 17-year period between the first and second surveys, the floods of December 1964 and January 1965 were of such magnitude that populations not occupying coverts remote from streams likely were eliminated or severely reduced in numbers. Thus, the 1970 survey (Verts et al. 1972) possibly was conducted after a major reduction in the cottontail range and before cottontails redispersed from coverts unaffected by the 1964–65 floods. Since 1970, however, flooding of riparian zones occurred only twice; no flooding occurred since January 1974 (Fig. 4). Although dispersal of cottontails likely was retarded and the range possibly reduced by floods during the early part of the decade between the second and third surveys, we believe that the 6 years since the last flood were adequate for cottontails to extend their range two and one-half fold (Fig. 1). High ground, not subject to flooding, and the

nearly continuous suitable cover provided along the railroad right-of-way adjacent to the North Santiam River (Fig. 3) may explain the extent of cottontail dispersal along the north boundary of our study area (Fig. 1).

Unoccupied Areas within the Range

Treatment of cottontail dispersion on the study area must include explanation of several relatively large areas seemingly unoccupied in 1980 that were occupied during earlier surveys (Fig. 1). The increase in size of the unoccupied area south of Albany since 1970 (Fig. 1) and the appearance of unoccupied areas south of Oakville and north of Harrisburg (Fig. 1) likely were related to loss of brushy coverts (Fig. 2). We found one or more coverts occupied by cottontails in 1953 or 1970 replaced by industrial complexes, warehouses, or condominiums. However, modification of most sites judged no longer occupiable by cottontails (Fig. 2) was related to agricultural practices, particularly removal of brushy fencerows.

Within the newly occupied range, cottontails were not found on ridge tops or in agricultural areas between major stream systems. We suspect that coniferous forests that exclude understories of brushy and grassy species make many ridge tops unsuitable for occupancy by cottontails. Disjunct brushy coverts in agricultural areas, although sufficiently large and of adequate quality to support cottontails, may not be occupied because intervening crops do not serve as suitable cover at seasons that juveniles disperse. These coverts may become occupied by cottontails in the future.

Also, a large area in the vicinity of Scio, searched, but seemingly not occupied by cottontails (Fig. 1), may be invaded in the future. We are unable to offer a plausible explanation for the absence of cottontails in the area, because Thomas Creek and Crabtree Creek (Fig. 3) should provide avenues for dispersal, and brushy fencerows interconnecting with riparian zones to support cottontails were relatively abundant. A small unoccupied area near Sweet Home (Fig. 1) seemed to support vegetative communities adequate for cottontails, but coverts suitable for cottontails were absent in much of the

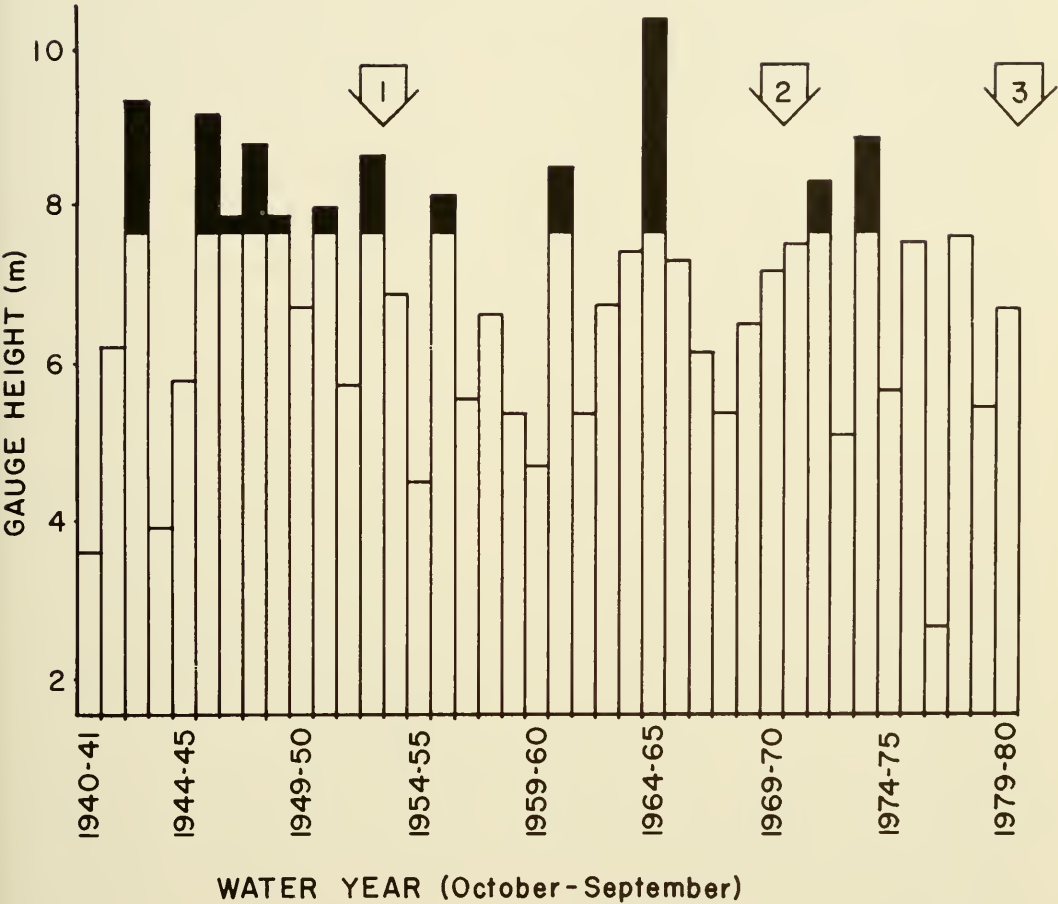


Fig. 4. Maximum gauge height for the Willamette River at Albany, Oregon, each water year, 1940-41 to 1979-80. Datum of gauge is 52.48 m above mean sea level. Solid portions of bars indicate height above flood stage (7.62 m) established by the U.S. Weather Bureau. Arrows indicate years that the three surveys of cottontail distribution were conducted. Hydrologic data are from Hulsing and Kallio (1964), U.S. Department of the Interior (1958-1978), and L. Hubbard, U.S. Geological Survey (pers. comm.).

unoccupied area south of Harrisburg, except for the narrow riparian zone along the Willamette River (Fig. 1).

Comparative Rates of Dispersal

The rate of dispersal of cottontails on our Linn County study area was infinitesimally slow in comparison with the more than 113 km per year that introduced European

rabbits (*Oryctolagus cuniculus*) averaged in New South Wales, Australia (Keast 1966). The disparity was especially great in view of differences in productivity reported for introduced populations of the two species; female European rabbits in Australia produced about 26 young in four or five litters during the annual breeding season (Myers and Poole 1962), whereas female cottontails in Oregon produced about 39 young in eight litters

(Trethewey and Verts 1971). Also, juvenile female cottontails older than 3.5 months commonly bred and some produced at least two litters during the breeding season in which they were born (Trethewey and Verts 1971), but confined populations of European rabbits were not reported to produce offspring in the season of their birth (Myers and Poole 1962), and, among wild populations, 95 percent of the productivity was by females more than six months old (Dunsmore 1971). In addition to having lower natality than cottontails, dispersing European rabbits in Australia were subjected to intensive control measures (Troughton 1943), whereas cottontails in Oregon have not become pests (Verts and Carraway 1980) and hunting of introduced cottontails has not become a popular sport (M. Henjum, pers. comm.).

Myers and Parker (1965) suggested that unoccupied burrow systems of the boodie (*Bettongia lesueuri*) preconditioned the habitat for warren-dwelling European rabbits and contributed to their rapid dispersal. Grizzell (1955), Linduska (1947), Hamilton (1934) and others documented the use of woodchuck (*Marmota monax*) burrows by cottontails and believed that burrows were important to survival of cottontails in the northern portion of their native range. The absence of a burrow-constructing ecological equivalent to *Bettongia* or *Marmota* west of the Cascade Range in Oregon possibly contributed to the slow rate of cottontail dispersal. However, use of burrows by cottontails in their native range usually was limited to inclement weather (Linduska 1947) more severe than occurs commonly in the Willamette Valley, Oregon.

ACKNOWLEDGMENTS

Our research was supported, in part, by an award from the Oregon State University Research Council. We are indebted to L. Hubbard, U.S. Geological Survey, for providing unpublished hydrologic data for 1978-79 and 1979-80. We thank our colleagues, J. A. Crawford and B. E. Coblenz, for critiques of the manuscript. This is Technical Paper 5635, Oregon Agricultural Experiment Station.

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THE 1900 INVASION OF ALIEN PLANTS INTO SOUTHERN IDAHO

Dana L. Yensen¹

ABSTRACT.— The European annual plants *Salsola iberica*, *Sisymbrium altissimum*, *Descurainia sophia*, and *Bromus tectorum* invaded southern Idaho about 1900 and spread very rapidly into native plant communities damaged or eliminated by burning, abusive grazing, and agricultural clearing. Historic photographs reveal that the sites of initial invasion were waterway margins, railroad rights-of-way, road shoulders, city streets, agricultural areas, and construction sites. By 1915, these plants were widespread and abundant. Burning and grazing fostered their spread and dominance on millions of acres in southern Idaho.

Several European annual plants invaded southern Idaho during the few years preceding and following the turn of the century. The spread of these alien plants, especially cheatgrass, was so rapid that it often escaped recording (Leopold 1941). Four important plants—*Salsola iberica* Sennen and Pau, *Sisymbrium altissimum* L., *Descurainia sophia* (L.) Webb., and *Bromus tectorum* L.—changed the ecology and the very appearance of southern Idaho. This paper presents some new information on documenting the invasion of these plants into southern Idaho, and the means by which they came to dominate millions of acres of desert rangeland.

PRESETTLEMENT VEGETATION

The presettlement vegetation of southern Idaho consisted largely of open-canopied communities of low-growing shrubs, especially big sagebrush (*Artemisia tridentata*), as well as winterfat (*Ceratoides lanata*), bitterbrush (*Purshia tridentata*), rabbit brushes (*Chrysothamnus* sp.), and shadscale (*Atriplex confertifolia*) and other salt-desert shrubs. Most of the Snake River Plain was dominated by communities of big sagebrush with a rich understory of perennial bunch grasses (*Stipa*, *Elymus*, *Agropyron*, *Oryzopsis*, *Poa*, and *Festuca*) and herbs (*Balsamorhiza*, *Hydrophyllum*, *Tragopogon*, and *Agoseris*), or by winterfat or other salt-desert communities (Townsend 1839, Fremont 1845, Irving 1907, Elliot 1913, Ferrin 1935, Keith 1938, Stover 1940, Vahlberry 1940, Platt and Jackman

1946, Blaisdell 1953, Root 1955, Shirk 1956, Fulton 1965, Ellison 1960, Vale 1975, Gibbs 1976, Hironaka and Fosberg 1979, Meacham 1979, Young et al. 1979). The perennial grasses and several of the shrubs, notably winterfat, saltbushes, and bitterbrush, are highly palatable and nutritious to grazing animals (Kennedy 1903, Hodgeson 1948, Hutchings and Stewart 1953, Ellison 1960).

Originally, if sagebrush grasslands were burned, trampled, or otherwise severely disturbed and left wholly or partially bare of vegetation, snakeweed (*Gutierrezia sarothrae*) would appear on the disturbed areas within a year or two (Stewart and Hull 1949). Establishment of snakeweed was followed by the appearance of the short-lived perennial grasses bottlebrush squirreltail (*Sitanion hystrix*) and Sandberg's bluegrass (*Poa sandbergii*), along with big sagebrush seedlings. Finally, the large-culmed perennial grasses and the perennial broadleaved herbs would appear (Ellison 1960, Young et al. 1972). Revegetation occupied about a decade, and only occurred if the area was not significantly disturbed. In southern Idaho at the turn of the century, however, continual disturbance by fire, abusive grazing, agricultural practices, and construction (railroads, roads, towns, canals) created an environment in which presettlement patterns of secondary succession could not persist unchanged (Kennedy 1903, Piemeisel 1938, 1951). The stage was set for the invasion of alien plants (Young et al. 1979).

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CONDITIONS LEADING TO THE INVASION OF EXOTIC PLANTS

By 1900, native plant communities had been severely damaged by overgrazing (Hodgeson 1948, Piemeisel 1938). Pickford (1932) wrote that in the 30 years after 1880, burning and abusive grazing had resulted in an 85 percent reduction in native perennial grasses and a 40 to 50 percent reduction in the carrying capacity of the range. By this time, stands of native perennial grasses had been virtually eliminated from southern Idaho desert lands (Hodgeson 1948). Burning also caused serious and widespread damage to the vegetation. Many stockmen, erroneously believing that burning the shrublands produced good stands of grasses even when grazing pressure following burning was not reduced, deliberately set range fires (Griffiths 1902, Pechanec and Hull 1945, Vale 1975). Griffiths (1902), who traveled southwestern Oregon ranges in 1901, reported that such range fires were very common, and that many of the fires were set by sheepmen. The fact that sheepmen used to set many range fires is common southern Idaho lore (Hicks pers. comm., C. L. Stewart pers. comm.).

From 1900 until the end of World War I, large numbers of prospective farmers settled in southern Idaho (Rinehart 1932, Gibbs 1976). In the words of Hultz (1934), the country was "wheat mad." Railroads offered cheap one-way home seeker fares, and many settlers took advantage of them (Stewart and Hull 1949, Gibbs 1976). Large acreages of sagebrush lands were settled and cleared for planting row crops and orchards. However, during the 1920s, an agricultural depression began in Idaho. Many farmers went bankrupt and abandoned their homestead claims (Stewart and Hull 1949, Gibbs 1976). Thousands of acres of plowed farmland, many acres of which had been dry-farm wheatfields, were left unattended (Warg 1938, Piemeisel 1938, Stewart and Hull 1949, Young et al. 1979).

Several decades of burning, trampling, overstocking, and abusive grazing not only severely damaged the perennial grass and herb understory of the big sagebrush lands, but also greatly reduced the acreage dominated by the most valuable forage shrub, winterfat. By 1900 many hundreds of

thousands of acres of big sagebrush remained, virtually bare of understory (Sweetser 1935, Chapline 1936, Stewart 1936, Taylor 1940, Hodgeson 1948, Reidl et al. 1964, Young et al. 1979). Erosion of the soil became a critical problem, both on the open range and on abandoned cropland (Clapp 1936, USDI-BLM 1974). And, with no easing of grazing pressure, rehabilitation of the weakened native plant communities was not possible (Young et al. 1979).

HISTORY AND ECOLOGY OF INVASION

RUSSIAN THISTLE.— Russian thistle, *Salsola iberica* Sennen and Pau (Beatley 1973), was probably the first important invading plant (Hutchings and Stewart 1953). This spiny and compact annual herb is a native of the desert-steppe region of Russia. Russian thistle germinates in late spring or early summer, grows during the summer, and dies in the fall. The aboveground part of the plant then breaks off and is tumbled along the ground by the wind, scattering seeds (Piemeisel 1938). These ball-shaped dead plants are the "tumbleweeds" of western cowboy lore. Russian thistle was commonly called "tumbleweed" in southern Idaho, but was not present during the heyday of the cowboy (Piemeisel 1938, Hicks pers. comm.). Russian thistle does not tolerate crowding of stands, and will not continue to grow on an area unless the area is continually disturbed. Therefore, the presence of Russian thistle indicates lands which have been severely or continually disturbed within the past one to three years (Piemeisel 1938).

Russian thistle invaded the western United States just before 1900 (Hutchings and Stewart 1953). In Idaho, the seeds of Russian thistle were probably distributed via the Snake River and were further disseminated by irrigation canals and field ditches, the bare margins of the newly constructed waterways being excellent sites for colonization (Dewey 1896). Also, seeds of Russian thistle may have been distributed in alfalfa and other crop seeds (Piemeisel 1938).

Because of its large size and distinctive appearance, Russian thistle is easily identified in photographs. Photographs on file in the collection of the Idaho Historical Society

(Boise, Idaho), document the early establishment of Russian thistle in southern Idaho. Figure 1 is an example. The earliest photographs of Russian thistle in Idaho are IHS 64044.3, showing the plants growing on a railroad embankment in southeastern Idaho in 1890; IHS 73-230.23, an 1897 photograph showing plants growing in Nampa at the foot of a speaking platform on which William Jennings Bryan was standing; and IHS 74-194.4a, taken in Roswell in 1898, showing Russian thistle growing near a newly constructed farmhouse. Other Idaho Historical Society photographs reveal that Russian thistle first became established on railroad rights-of-way; on the edges of (dirt) city streets and in vacant city lots; at construction sites of buildings, bridges, and roads; in agricultural waste places and on field margins; and near waterways. At least 50 early photographs taken in southern Idaho show that Russian thistle was well established and widely distributed in southern Idaho by 1905, and was abundant by 1915. The fact that Russian thistle rapidly invaded severely disturbed big

sagebrush lands is illustrated by IHS photograph 73-221.810, taken in 1909 near Twin Falls, which shows a newly constructed church surrounded by a big sagebrush community with only a small cleared space in front of the building. The cleared area supports hundreds of Russian thistle plants, and the photograph is labeled "Three months from sagebrush."

In addition to mechanical disturbance (construction, grazing), fire also helped to establish Russian thistle in southern Idaho. Following burning, Russian thistle became the first plant to colonize newly burned lands, rapidly invading burned big sagebrush-perennial grass areas before snakeweed or other native plants could gain a foothold (Piemeisel 1938, Stewart and Hull 1949).

Russian thistle, though inferior in palatability and nutritional value to native grasses, can be used as forage by livestock. When it first appeared in abundance on the southern Idaho range, it was hailed by stockmen as a valuable new forage plant (Leopold 1941). Russian thistle can only be used by



Fig. 1. *Salsola iberica* and *Sisymbrium altissimum* (foreground). "Green's ranch," 24 August 1909, near Nampa, Canyon County, Idaho. Photograph courtesy of the Idaho Historical Society.

livestock, however, in the summer, before it dries into a spiny skeleton (Murray and Klemmedson 1968).

MUSTARDS.—Several European members of the mustard family also invaded disturbed southern Idaho lands. The most important of these were tansymustard (*Descurainia sophia* (L.) Webb.) (Detting 1939) and tumbledustard (*Sisymbrium altissimum* L.). These annual mustards bloom from early spring to early summer, after which they dry and die. Like Russian thistle, they have short taproots and do not protect the soil from erosion (Hull and Pechanec 1947). Tumbledustard may also break off and scatter seeds in the fall. Tumbledustard was also called “tumbleweed” in southern Idaho, but not as commonly as was Russian thistle (Hicks, pers. comm.). Mustards can tolerate more crowded conditions than Russian thistle and can persist in very dense stands for a few years, but not indefinitely. Peak demands by these plants on upper soil moisture occur before Russian thistle begins to grow. These characteristics enable the mustards to invade Russian thistle stands and replace the Russian thistle within one to three years, if not severely disturbed. However, if a mustard stand is heavily trampled or otherwise disturbed, Russian thistle will replace the mustards. Mustard stands become extremely crowded in a few years and cannot persist. If not disturbed, mustards will soon be invaded and replaced by other plants (usually cheatgrass) (Piemeisel 1951, Hironaka and Tisdale 1963).

The mustards, less distinctive in habit than Russian thistle, are much more difficult to identify with certainty in photographs. The first evidence of tumbledustard growing in Idaho is Idaho Historical Society photograph IHS 73-230.23, showing tumbledustard (with Russian thistle) in Nampa in 1897. Four 1906 Idaho Historical Society photographs show tumbledustard present along man-made waterways near Jerome and Twin Falls (IHS 73-221.781c, IHS 60-176.103, IHS 60-176.104, IHS 60-176.106). Tumbledustard also appeared between 1900 and 1917 along railroad tracks, on roadsides, at construction sites, and in agricultural areas (Fig. 1). Tansymustard is even more difficult to recognize in photographs; it probably became established at about the same times and in the

same places as did tumbledustard. The first reliable photograph evidence of tansymustard in southern Idaho is IHS photograph 68-05.45, taken at Massacre Rocks State Park along the Snake River in 1916. The mustards were widespread in Idaho by 1915. Weaver (1917:110) wrote that at that time tumbledustard or “Jim Hill mustard,” as it was then called, was “present to a degree almost unbelievable.” He stated that it has been introduced into the Pacific Northwest along railroad rights-of-way. Piemeisel (1938) reported that seeds of pinnate tansymustard and tumbledustard were distributed in alfalfa seed. These mustards also invaded depleted rangeland. They are unpalatable to livestock, a fact that favored their establishment and spread (Kennedy and Doten 1901).

CHEATGRASS.—The most important exotic annual to invade Idaho was the Mediterranean winter annual grass *Bromus tectorum* L., which in the West has been called cheatgrass, cheatgrass brome, downy brome, downy chess, Junegrass, bronco grass, and Mormon oats. Cheatgrass now occurs in every state except Alabama, Georgia, South Carolina, and Florida. In the eastern states it is a roadside weed, but in the West it has invaded millions of acres of rangeland and cropland (Hull and Pechanec 1947, Stewart and Hull 1949, Klemmedson and Smith 1964).

Cheatgrass germinates during fall rains and maintains small, dormant leaves during the winter. In spring, it grows rapidly and begins to form seed heads in April. In May, the seeds mature, and the plants turn purplish as they dry in the early summer heat. In June and July the seeds mature and fall to the ground, and the plants die. The dry plants, by then straw colored, persist upright in place for months (Stewart and Hull 1949, Klemmedson and Smith 1964).

Stewart and Young (1949) noted that cheatgrass was collected in Pennsylvania in 1861, in Washington in 1893, in Utah in 1894, in Colorado in 1895, in Wyoming in 1900, and was present in nearly all of its current range by 1900, though it was not as abundant as it was later to become. Stewart and Young implied that the spread of cheatgrass was from east to west. However, there is a strong possibility that the first cheatgrass

to arrive in Idaho came from awns carried in the coats of sheep trailed from California through Nevada to southern Idaho.

Cheatgrass awns catch in the coats of livestock and may be carried for miles before dropping out (Piemeisel 1938). The first instances of cheatgrass invasion in Nevada were in areas where California sheep had grazed (Kennedy 1903). Since bands of California sheep were trailed through Nevada and into Idaho (Wentworth 1948, Hanley and Lucia 1973), it seems reasonable to assume that cheatgrass awns could have been carried into Idaho by these sheep. Piemeisel (1938) notes that, as with other exotic annuals, cheatgrass seeds were often present in alfalfa seeds, and cheatgrass was also distributed in that way. An Idaho Historical Society photograph (IHS 503-F), taken at the mouth of Kuna Cave in southern Ada County in 1898, shows a dense stand of cheatgrass growing under a sparse cover of big sagebrush. This is the earliest photographic evidence of cheatgrass occurrence in Idaho, and even at the time of the photograph it appears to have been well established. Klemmedson and Smith (1964) note that cheatgrass is included in Piper and Beattie's 1907 *Flora of the Palouse*, Howell's 1903 *Flora of Northwest America*, and Piper's 1906 *Flora of Washington*. Cheatgrass, however, is not mentioned in Weaver's (1917) *Flora of South-eastern Washington and Adjacent Idaho*.

O. R. Hicks (pers. comm.) remembered that, just prior to 1906, cheatgrass occurred in south central Idaho between the towns of Glens Ferry and King Hill in what was called a "railroad line"—a line of cheatgrass invasion originating on the railroad right-of-way and extending about 300 yards into the native vegetation on either side of the railroad tracks. Hicks believed that cheatgrass was fed to the sheep in the stock cars and that seed heads fell from the cars to ground along the tracks.

In the first few years after 1900, cheatgrass gained a foothold on disturbed areas such as railroad rights-of-way, road shoulders, orchards, fallow fields, and especially in dryland alfalfa fields which were grazed after having been harvested (Stewart and Hull 1949). In photographs, cheatgrass is not distinctive in appearance at a distance and can

be positively identified only in uncommon instances. It is undoubtedly present in many photographs where reliable identification is not possible. (Cheatgrass is a relatively small, fine-textured plant, and its delicate heads are stirred by a slight breeze, often blurring the photographic image.) Idaho Historical Society photographs in which cheatgrass can be positively identified show cheatgrass to have been present in southern Idaho by 1910 in areas along railroad rights-of-way, on roadsides, and in vacant, disturbed areas within towns. Severely damaged rangeland was also invaded about this time (Stewart and Hull 1949).

Cheatgrass has been called an aggressive invader of big sagebrush lands (Platt and Jackman 1946), but Piemeisel (1938), who did classic successional studies in southern Idaho beginning in the 1920s, concluded that invasions of big sagebrush lands by cheatgrass were largely limited to voids in native vegetation. Warg (1938) concluded that cheatgrass could not invade pristine native vegetation and that invasion by cheatgrass was an indication of disturbed range. Young et al. (1979) also felt that exotic annuals, including cheatgrass, did not invade stands of healthy native vegetation.

Many stockmen were enthusiastic about the appearance of the abundant new grass, and erroneously believed it to be superior to the native perennials it had replaced (Stablein 1940, Platt and Jackman 1946). Even though cheatgrass was a poor substitute for the native grasses, at the time of its rapid establishment and spread it was a blessing for the range because it did afford quantities of forage for livestock held on depleted ranges, and afforded some protection from soil erosion when much of the range was overgrazed and denuded of soil cover (Platt and Jackman 1946).

Cheatgrass burns. Because cheatgrass is the most inflammable of the range forage plants, range fires in southern Idaho became more frequent. Cheatgrass range is 500 times more likely to burn than any other rangeland type (Platt and Jackman 1946, Stewart and Hull 1949). Leopold (1941) wrote that it is in fact impossible to protect cheatgrass ranges from fire. Burning is very damaging to big sagebrush-grass communities (Pechanec et al.

1954, Vale 1974). The presence of cheatgrass in these communities can carry fires into areas that would normally not burn (Stewart and Hull 1949, Hull 1965, Pechanec et al. 1954).

Many early stockmen believed that fire did not damage cheatgrass stands (Stablein 1940, Pechanec and Hull 1945), since, once established on an area, cheatgrass will be present the year after it has been burned because cheatgrass seeds are not usually all destroyed by fire (Warg 1938, Leopold 1941). Many southern Idaho stockmen regularly set range fires, because the following year the burned areas were not camouflaged by shrubs or by the previous year's dried growth and so appeared greener (Hicks pers. comm.). Cheatgrass on the range increased very rapidly when fire was combined with overgrazing, which was often the case (Stewart and Young 1939, Leopold 1941, Ellison 1960, Hironaka and Fosberg 1979). Cheatgrass replaced much vegetation on burned areas and came to dominate millions of acres, aided by its own flammability (Stewart and Hull 1949, Klemmedson and Smith 1964, Hironaka and Fosberg 1979).

After cheatgrass became well established in southern Idaho, the pattern of secondary succession was changed. No longer was an initial disturbance necessarily followed by the eventual appearance of native shrubs and grasses. After the invasion of the exotic annuals, the secondary succession pattern became Russian thistle invasion initially, followed by mustard invasion, and finally by cheatgrass establishment. Russian thistle dominated for a year or two, mustards for two or three years, and then cheatgrass became the dominant species (Piemeisel 1951, Hironaka and Tisdale 1963). If undisturbed, cheatgrass stands were in turn invaded by bottlebrush squirreltail and subsequently by other native plants (Hironaka and Tisdale 1963). However, if cheatgrass were burned or grazed, it was able to maintain itself indefinitely (Piemeisel 1938, 1951). Overgrazing combined with burning helped to insure a continuous stand of cheatgrass and to prevent reestablishment of native plants (Piemeisel 1938, 1951, Leopold 1941, Stewart and Hull 1949).

In the years immediately following World War I, cheatgrass made its most rapid advances, colonizing millions of acres of abandoned farmland and disturbed range (Piemeisel 1938, Wentworth 1948, Stewart and Hull 1949). By the late 1920s cheatgrass was abundant in southern Idaho. An *Idaho Statesman* article dated 1 May 1928 reported that the desert bunchgrass had been replaced by grass that "grows in a day, ripens in a day, and blows away in a day." By 1932, the most important plant on Idaho desert ranges was cheatgrass (Rinehart 1932). By 1949, about 4,000,000 acres in Idaho were dominated by cheatgrass, and cheatgrass was an important component of the vegetation on 10,000,000 to 15,000,000 additional Idaho acres (Stewart and Hull 1949). This plant is now the most important forage plant in Idaho (Klemmedson and Smith 1964). The impact of cheatgrass is difficult to comprehend, for it has literally changed the appearance of southern Idaho (Young et al. 1979).

SUMMARY

At the turn of the century, the alien annual plants Russian thistle, tansymustard, tumble-mustard, and cheatgrass invaded the native plant communities of southern Idaho after having first become established on canal banks, city streets, construction sites, road shoulders, abandoned farmlands, and railroad rights-of-way. Abusive grazing and burning weakened the native plant communities and opened the vegetation to invasion by these plants. The alien plants changed the patterns of secondary succession in southern Idaho and also altered the carrying capacity of the range, the amount of soil erosion, and the frequency of fires. Continued burning and excessive grazing allowed these annuals to become dominant on millions of acres of land in southern Idaho. The face of southern Idaho has been changed by the invasion of these exotic plants.

ACKNOWLEDGMENTS

I thank Graham Smith for his guidance and support during the course of this research. Tom Kucera, Robert Smith, and Karen Steenhof critically read the manuscript and offered

useful suggestions. The assistance of Katherine Bettis, Jane Houston, Ann Joslin, and others of the Idaho State Library was of great value in locating sources. John Lamborn of the Merrill Library, Utah State University, aided me in using the Works Progress Administration History of Grazing files and gave me access to the Stoddart literature collection. The Idaho Historical Society allowed me to use their extensive photograph file and to reprint the photograph that appears herein. This research was supported by USDI-BLM Contract 52500-CT5-1002, Dr. Donald R. Johnson, principal investigator, Department of Biology, University of Idaho, Moscow.

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A SAGEBRUSH WILT DISEASE OF UNKNOWN CAUSE

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ABSTRACT.— A sagebrush wilt disease is causing severe damage to Forest Service uniform shrub garden plantings in Utah. Plants within most species of the section *Tridentatae* express disease symptoms and may die within several months. Varying degrees of susceptibility are evident within and between species. Modification of the soil environment through past agricultural use may dispose these wildland shrubs to associated potentially pathogenic fungi.

A sagebrush (*Artemisia* L.) disease of unknown cause is severely damaging USDA-Forest Service uniform shrub garden plantings at the Utah State University Snow Field Station at Ephraim, Utah. Although the disease is not known to occur in the wildland situation, it is important from at least two aspects. First, it renders growing and maintaining the uniform shrub gardens almost impossible. Second, decimation of selected population accessions greatly depletes the genetic base. Evaluation and selection of plants for desirable characteristics such as productivity, nutritional value, drought tolerance, winter hardiness, disease resistance, and so forth are thus on a less firm basis. Assemblage of plant materials in uniform plantings is the initial step in the Forest Service's wildland shrub improvement program. The program is a cooperative effort of the USDA-Forest Service, Utah State Division of Wildlife Resources, and Utah State University.

Artemisia is a major component of the vast western United States shrublands (Beetle 1960, McArthur and Plummer 1978). Among the members of this aggressive, diverse, and adaptable genus are species useful for restoring depleted ranges and disturbed landscapes (McArthur et al. 1974, Monsen 1975), for providing nutritious and palatable browse on western big game and livestock ranges (Plummer et al. 1968, Welch and McArthur 1979), and for habitat of numerous other forms of wildlife (McKell et al. 1972).

MATERIALS AND METHODS

Assemblage of plants at the Snow Field Station began in the late 1960s and has continued to the present. The *Artemisia* selections were collected primarily from the Great Basin. Others were obtained from surrounding areas in Arizona, Colorado, Idaho, Utah, and Wyoming. Accession sources for the same species or subspecies, with few exceptions, were from different origins in each of the different years of planting. All entries of the same year were placed in the same section of the garden with those of subsequent years in adjoining sections. Entries were made as young wildling transplants. After initial watering to encourage establishment, no supplementary water was given. The plantings were cultivated to control weeds.

The number of plants established following transplant was determined at the end of the first season. Thereafter annual observations were made on plant development. The number of plants within each accession was highly variable because of transplant loss and the number available at the collection sites. Observations on disease development were not begun until 1974. The accession entries made from 1968 through 1971 appeared to be the most comparable and were selected for a disease survey in the fall of 1978. The number of plants surviving without advanced wilt symptoms was determined for each accession.

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The range in percentage survival was calculated from individual accessions within years and the mean percentage from a total of all accessions within species for each year. The total percentage survival representing accession totals for all years was totaled for each species. The more or less miscellaneous array of differing sources and numbers within and between species each year allowed only a general statistical comparison.

RESULTS

Observations revealed the following general pattern of disease development. First symptoms of the disease usually occurred in late fall or early spring as wilted leaves and shoot tips (Fig. 1). By midsummer, portions (Fig. 2A) or entire plants (Fig. 2B) collapsed and died. The disease occurred in young well-established plants during their first season of growth and in plants one or more years old. In one planting, there was a high incidence of wilt and death of plants during

the second season that subsided but continued to occur at a reduced rate in following years. Plants died out in patches (Fig. 3A), but more commonly there was a scattered pattern of dying (Fig. 3B).

A pronounced bluish green vascular discoloration, symptomatic of a *Verticillium*-induced disease of woody plants (Bedwell and Childs 1938, Caroselli 1957), was associated with some dying plants; however, the discoloration also occurred with non-wilted plants. Portions of the root systems of some wilt-diseased plants were necrotic, but death of plants did not seem to be associated with earlier advanced root rot or decay. It was not obvious where and how the disease was initiated in the plants. Usually, for example, when half the crown wilted and died, the corresponding portion of the root system was also found dead. Death from a vascular wilt pathogen rather than from winter injury appeared more probable because of the lack of a marked increase in rate or intensity of kill immediately following colder and drier winters and the typical wilt disease symptoms expressed by some plants during the first season planted.

All members of the section *Tridentatae* (see taxonomy in Beetle 1960, Beetle and Young 1965) exhibited symptoms except *A. pygmaea*, *A. longiloba*, *A. rigida*, and *A. spinescens* (Table 1). The latter three species were represented by only a few plants and therefore were not listed in Table 1. Species representing other sections of *Artemisia* did not express wilt symptoms and, except for *A. filifolia*, which was represented by only a small number of plants, survived to a relatively high degree compared to the *Tridentatae* in general. *Artemisia ludoviciana* and especially *A. abrotanum* seem to have suffered the least loss. Within the remaining *Tridentatae*, survival appeared to be the highest with *A. arbuscula* and *A. nova*, intermediate with *A. tridentata*, and lower with *A. bigelovii*, *A. cana*, and *A. tripartita*; the most severely affected was *A. rothrockii*. Within *A. tridentata*, which is of special interest to the project, ssp. *tridentata* (valley or basin big sagebrush) appeared to be somewhat less affected than ssp. *vaseyana* (mountain big sagebrush). The other subspecies, *wyomingensis* (Wyoming big sagebrush), probably cannot



Fig. 1. Wilt disease symptoms on *Artemisia tridentata*. Note wilted leaves and shoot tips (arrow).

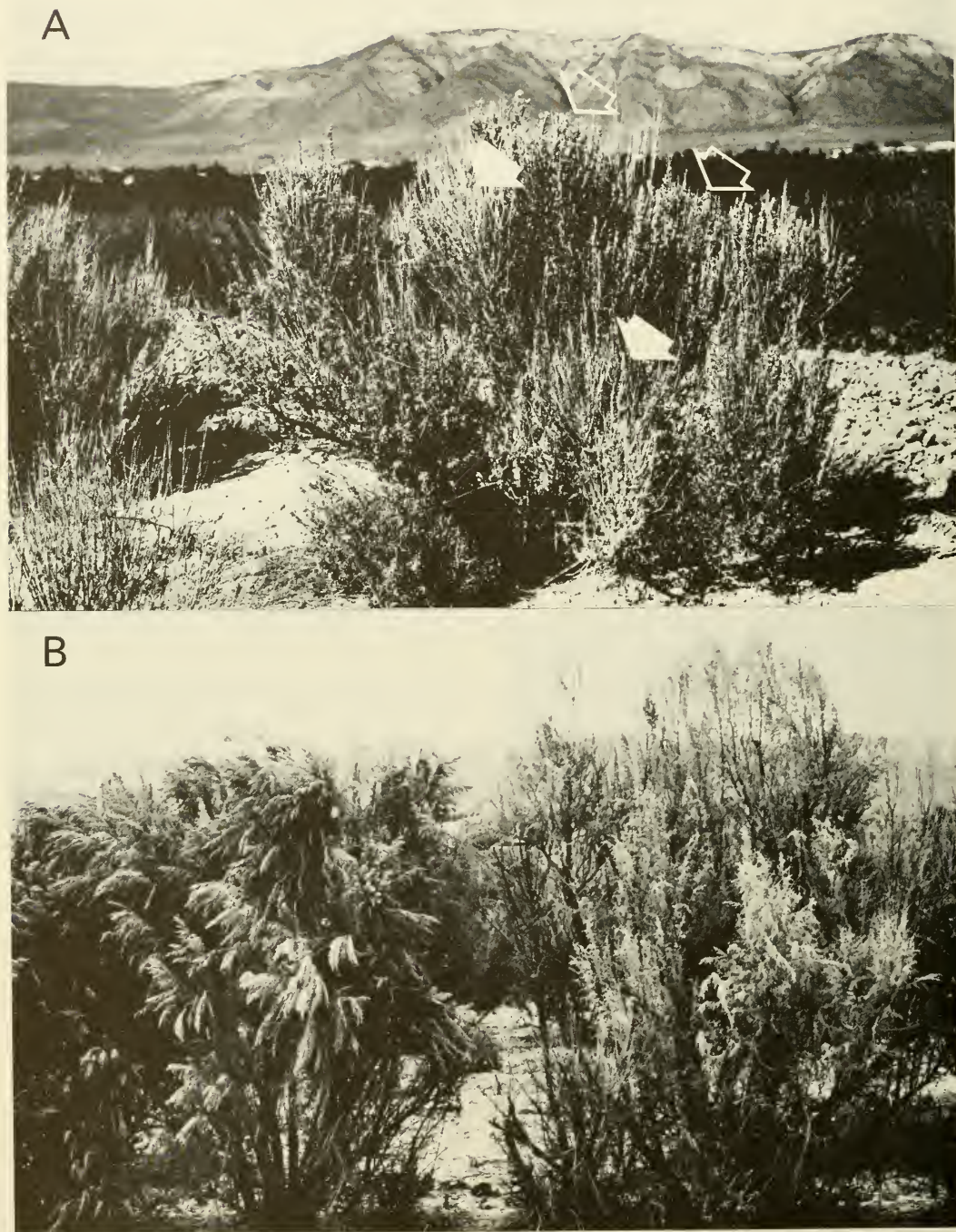


Fig. 2. Pattern of dying from wilt disease in individual plants. A, Partial death of *A. tridentata* ssp. *vaseyana*, Spring City, Utah, source. Open arrows mark living portions, closed arrows mark dead portions of plant. B, Death of entire plant on right occurred by midsummer. Dove Creek, Colorado, source of *A. tridentata* ssp. *tridentata*. Plants are about 2.5 m tall. Drooping appearance of plant on left is from heavy floral heads.



Fig. 3. Pattern of dying from wilt disease in shrub garden plantings. A, A patch of dying plants. Photo taken during third season of planting, Snow Field Station. B, Scattered death of plants of various accessions. Photo was taken during fourth season of planting, Snow Field Station.

be compared reliably because of the small number of plants. Accessions within most species appeared to vary markedly in survival rates (see "percent survival" ranges, Table 1), and there tended to be a continuous death with time (see survival amounts of plants established, 1969-1972, Table 1).

The annual loss of *A. tridentata* was followed in another planting established in 1975 in a different area of the Snow Field Station. Plants grew vigorously throughout the observation period. Starting from one-year-old seedling transplants, at the end of the first season ssp. *tridentata* averaged 55 cm (Dove Creek source 60 cm) and ssp. *wyomingensis* and ssp. *vaseyana* 34 cm in height. Readings were made each fall through 1978 on the number of plants expressing wilt symptoms and dying from the disease. The results are summarized in Table 2. Loss of plants through midsummer of the first season was attributed to transplant injury. September through November, plants began developing wilt symptoms, and most of these died early in spring 1976. After the second season, little additional death of the *A. tridentata* ssp.

tridentata accessions occurred. With the other subspecies additional deaths occurred but in somewhat lesser amounts each year. By the end of the 1978 season only 58.8 percent of the three *A. tridentata* ssp. *vaseyana* accessions survived. Survival in *A. tridentata* ssp. *wyomingensis* and *A. tridentata* ssp. *tridentata* was 75.3 percent and 90.1 percent, respectively.

DISCUSSION

Wilt disease symptoms were associated with most of the severe loss of plants recorded in Table 1. This loss cannot be attributed entirely to the disease since observations of the disease were not documented during early years of the plantings. In some accessions, especially with larger plant species, the spacing turned out to be too close and competition for water, light, and nutrients likely contributed directly to their death.

In its virgin state, the Snow Field Station area was a big sagebrush (*Artemisia tridentata*), black greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.), and bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn.

TABLE 1. Loss of *Artemisia* plants at the Ephraim shrub garden.

<i>Artemisia</i> species	Year established	No. of accessions	Number established	No. without wilt in 1978	Range and mean ^a survival (%)	
SECTION TRIDENTATAE						
<i>A. arbuscula</i> Nutt.	1969	4	50	2	0.0 (4.0)	9.1
	1970	1	106	15	(14.2)	
	1971	2	87	9	8.8 (10.3)	11.9
	1972	3	165	161	62.5 (97.6)	100.0
			408	187	45.8	
<i>A. bigelovii</i> Gray	1970	5	203	9	0.0 (4.4)	7.7
	1971	4	54	2	0.0 (3.7)	18.2
	1972	4	82	29	0.0 (35.4)	52.8
			339	40	11.8	
<i>A. cana</i> Pursh	1969	2	4	0	(0.0)	
	1970	1	34	5	(14.7)	
	1971	3	138	15	5.5 (10.9)	19.1
	1972	1	20	0	(0.0)	
			196	20	10.2	
<i>A. nova</i> Nelson	1969	6	120	16	0.0 (13.3)	37.5
	1970	4	76	19	15.2 (25.0)	28.6
	1971	9	171	100	0.0 (58.5)	100.0
	1972	4	238	121	0.0 (50.8)	80.8
			605	256	42.3	
<i>A. pygmaea</i> Gray	1969	1	46	0	(0.0)	
	1970	1	36	6	(16.7)	
			82	6	7.3	

^aThe three figures represent the range and mean (center) percentage survival of the individual accessions for each year. The "total" percentage survival is of the total number of plants for all years sampled.

Table 1 continued.

<i>Artemisia</i> species	Year established	No. of accessions	Number established	No. without wilt in 1978	Range and mean ^a survival (%)	
<i>A. rothrockii</i> Gray	1969	2	196	12	1.5 (6.1)	15.9
			196	12	6.1	
<i>A. tridentata</i> Nutt. ssp. <i>tridentata</i>	1969	13	283	35	0.0 (12.4)	53.3
	1970	3	50	11	0.0 (22.0)	25.6
	1971	9	352	155	0.0 (44.0)	64.0
	1972	2	17	2	0.0 (11.8)	20.0
			702	203	28.9	
<i>A. tridentata</i> Nutt. ssp. <i>vaseyana</i> (Rydb.) Beetle	1969	1	18	0	(0.0)	
	1970	3	146	39	3.6 (26.7)	36.8
	1971	13	420	54	0.0 (12.9)	28.6
	1972	15	992	324	8.3 (32.7)	80.7
			1576	417	26.5	
<i>A. tridentata</i> Nutt. ssp. <i>wyomingensis</i> Beetle & Young	1969	3	27	1	0.0 (3.7)	20.0
	1970	2	51	1	0.0 (2.0)	2.0
	1971	4	66	17	0.0 (25.8)	39.5
	1972	2	16	11	0.0 (68.8)	73.3
			160	30	18.8	
<i>A. tripartita</i> Rydb.	1969	2	55	5	7.3 (9.1)	14.3
	1972	2	23	5	0.0 (21.7)	31.3
			78	10	12.8	
OTHER SECTIONS						
<i>A. abrotanum</i> (Bess) Rydb.	1972	1	161	154	(95.7)	
			161	154	95.7	
<i>A. filifolia</i> Torr.	1971	2	9	1	0.0 (11.1)	16.7
	1972	1	8	3	(37.5)	
			17	4	23.5	
<i>A. frigida</i> Willd.	1969	1	6	0	(0.0)	
	1970	2	73	6	3.2 (8.2)	36.4
	1971	4	128	80	0.0 (62.5)	89.9
	1972	1	32	17	(53.1)	
			239	103	43.1	
<i>A. ludoviciana</i> Nutt.	1970	2	64	31	44.4 (48.4)	51.4
	1971	2	49	48	83.3 (98.0)	100.0
			113	79	69.9	

and Smith) site. The soil is a heavy alluvial clay derived from limestone parent material. Although the physical and mineral nutrient characteristics have probably been altered to some extent by agricultural use, these factors do not appear to be a major or direct cause of the disease. The majority of plant accessions in the gardens were made as wildling transplants and, after establishment, their growth in general was vigorous to exceptional.

Artemisia spp. are known to form vesicular-arbuscular mycorrhizal associations (Wil-

liams and Aldon 1976, Williams et al. 1974) and may also form ectomycorrhizae. Interference with or lack of their formation in the uniform shrub gardens could lead to a nutritional deficiency from lack of proper nutrient adsorption (Voigt 1969). Some soil factors thought to influence formation of mycorrhizae include temperature, moisture, aeration, pH, organic and inorganic nutrients, fungal and plant exudates, and the rhizosphere biota (Slankis 1974). How the past agriculture may have altered these factors relative to *Artemisia* mycorrhizae is unknown.

TABLE 2. Death of *Artemisia tridentata* subspecies from the sagebrush wilt disease^a.

Subspecies	Accession source	No. planted spring 1975	No. surviving ^b				Survival ^c (%)
			1975	1976	1977	1978	
<i>A. tridentata tridentata</i>	Dove Creek, Colorado	100	87	82	80	78	89.7
<i>A. tridentata tridentata</i>	Bonanza, Utah	25	24	24	22	22	91.7
<i>A. tridentata wyomingensis</i>	Trough Springs, Nevada	75	73	68	60	55	75.3
<i>A. tridentata vaseyana</i>	Excel Canyon, Utah	132	131	84	80	79	60.3
<i>A. tridentata vaseyana</i>	South of Brigham Canyon, Utah	100	100	80	75	68	68.0
<i>A. tridentata vaseyana</i>	Hobble Creek, Utah	100	99	79	66	47	47.5

^aPlanting located at Snow Field Station.^bNumber of plants surviving in the fall of each year.^cPercentage survival is of those plants surviving transplant in fall 1975.

The presence of mycorrhizae on sagebrush in the shrub gardens has not been determined, but growth of affected sagebrush was vigorous on the site prior to the disease, indicating a mycorrhizal presence or adequate nutrition in its absence. Even though nutrition and other growth factors appear to be adequate, lack of mycorrhizal formation may dispose the plants to disease through the lack of protection it may provide against pathogenic microorganisms (Zak 1964).

Sagebrush has a loose exfoliating outer bark, and older stems split easily, commonly separating at annual growth junctures. Sagebrush also has a low branching habit, with main branches commonly originating just above the root-stem transition zone. The lower branches split readily, adaxially, from the main stem. The bases of some lower branches die, apparently from shade suppression, and their decay extends to the heart of the main stem. These characteristics possibly dispose the plant to pathogens. During approximately 100 years of agricultural use, which was primarily for forage and grain crop production, the composition of soil microorganisms has undoubtedly changed and is artificial to the native *Artemisia* rhizosphere. Any soil-borne plant pathogens and resulting diseases confronting *Artemisia* in the plantings could very well be artifacts of the previous agriculture.

Exploratory isolation trials have yielded a multitude of microorganisms, including bacteria, fungi, and nematodes. Because surface sterilants do not contact saprophytic-type organisms within outer bark and other dead tissue, distinction of parasitic pathogens and saprophytes is confused during isolation attempts. Fungal species of the genus *Fusarium*

and a verticillate *Gliocladium* were commonly isolated from living root and stem segments of diseased plants. *Sclerotinia* and *Rhizoctonia* were occasionally isolated from the upper root zone and the latter also was isolated from higher in the stems. Many soil-borne saprophytes and important parasitic plant pathogens exist within these genera (Walker 1969). Species of ordinarily saprophytic fungi such as *Alternaria*, *Ulocladium*, and *Cylindrocarpum* were commonly encountered. Isolation and inoculation studies are being made in an effort to establish the cause of the disease.

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A NEW VARIETY OF *CENTAURIUM NAMOPHILUM* (GENTIANACEAE)
FROM THE GREAT BASIN¹

C. Rose Broome²

ABSTRACT.—An expression of *Centaurium namophilum* (Gentianaceae), long confused with *C. exaltatum* in the Great Basin of the western United States, is described and designated as var. *nevadense*. It may be separated from the Death Valley region endemic, var. *namophilum*, by its broader leaves, its diffuse corymbose cyme, the ultimate peduncles that are longer than the flowers, its medium to deep rose pink corolla, and its stamens that equal or exceed the style and are only slightly exerted from the corolla-tube. The var. *nevadense* occurs from eastern California to western Utah, and from southeastern Oregon and adjacent Idaho south to the northern Mojave Desert of southeastern California. *Centaurium exaltatum* may be distinguished from the new variety by its broader, more elliptical leaves, dichotomous peduncles, paler pink or bluish and generally four-merous flowers, shorter and more blunt corolla lobes, and a thicker, more included style and stigma.

A phase of the Death Valley region endemic, *Centaurium namophilum* Reveal, Broome & Beatley (Gentianaceae), has been found growing around various desert springs and seeps in the Great Basin of east central California, Nevada, western Utah, southwestern Idaho, and southeastern Oregon. This variety often occurs in close sympatry with *C. exaltatum* (Griseb.) W. F. Wight ex Piper and has been confused with that species.

***Centaurium namophilum* Reveal, Broome & Beatley var. *nevadense* Broome, var. nov.** A var. *namophilo* caulibus gracilioribus, ramificatione corymbosa diffusa ascendentiore, corollis brevioribus roseis, stylis quam staminibus vulgo brevioribus differt. Chromosomatum numerus $n=17$ de typus. Typus: NEVADA: Esmeralda Co.: Gap Springs, 2.8 miles southeast of intersection of Nevada Highway 3A and U.S. Highway 6, T.1N., R.36E., sec. 6, ca 4600 ft elev., 22 Aug 1978, Broome 2388. Holotype, CAS; isotypes, 18 duplicates to be distributed from MARY.

Margins of alkaline springs and seeps or graminoid meadows from Inyo and Mono Counties, California, eastward across central and northern Nevada to western Utah, and northward into southwestern Idaho and southeastern Oregon, mostly from 2200 to 6000 ft elevation. Flowering from late June to September (Figs. 1, 2).

ADDITIONAL COLLECTIONS SEEN.—CALIFORNIA: Inyo Co.: 4 mi N of Lone Pine along U.S. Hwy. 395 at alkali spring on E side of rd at S entrance to Alabama Hills Scenic Route just N of Alabama Gate, 15 Jul 1978, Broome *et al.* 2281 (CAS and 19 duplicates); Owens Valley, N of Lone Pine, just above Alabama Gates, 3700 ft, 22 Jul 1973, DeDecker 3300 (CAS, RSA); E side of Fish Slough, T.6S., R.33E., sec. 6, 4185 ft, 15 Jul 1976, DeDecker 4103 (DEDECKER); alkaline meadow between Mono Co. line and Laws, 19 Jul 1952, Ferris 12552 (CAS, DS, US); Teck (Texas?) Springs, Funeral Mts., Death Valley, 27 Apr 1935, Gilman 1416 (US); shores of Owens Lake, 3600 ft, 5 Jun 1906, Hall & Chandler 7326 (UC); alkali marsh, Fish Slough, 8.5 mi N of Bishop, 2 Sep 1949, Nobs & Smith 1789 (UC); Furnace Creek, 17 May 1915, Parish 10035 (UC); E side of Fish Slough, T.6S., R.33E., sec. 6, ca 4150 ft, 23 Jul 1976, Reveal 4580 (MARY and 4 duplicates). Mono Co.: Fish Slough, T.5N., R.33E., sec. 31, 15 Jul 1978, Broome *et al.* 2282 (MARY and 6 duplicates); Fish Slough, 1.9 mi N of BLM Springs, T.5N., R.33E., sec. 19, 15 Jul 1978, Broome *et al.* 2283 (CAS and 5 duplicates); E side of Fish Slough, T.5S., R.33E., sec. 31, 17 Jul 1978, Broome & Reveal 2284 (CAS and 17 duplicates); Fish Slough, BLM Springs, T.5S., R.33E., sec. 30, 4200 ft, 30 Sep 1974, DeDecker 3697 (CAS); Fish Slough,

¹Field and herbarium work on this project has been supported by National Science Foundation Grant DEB-7921165.

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Fig. 1. *Centaurium nanophilum* var. *nevadense*. a,b, habits of two typical mature plants; c, top view of five-merous flower; d, mature capsule with persistent style; e, one valve of fruit showing the degree of placental intrusion into locule and mature seeds within; f, four-merous flower in side view. (Illustration by Peggy K. Duke of the University of Maryland.)

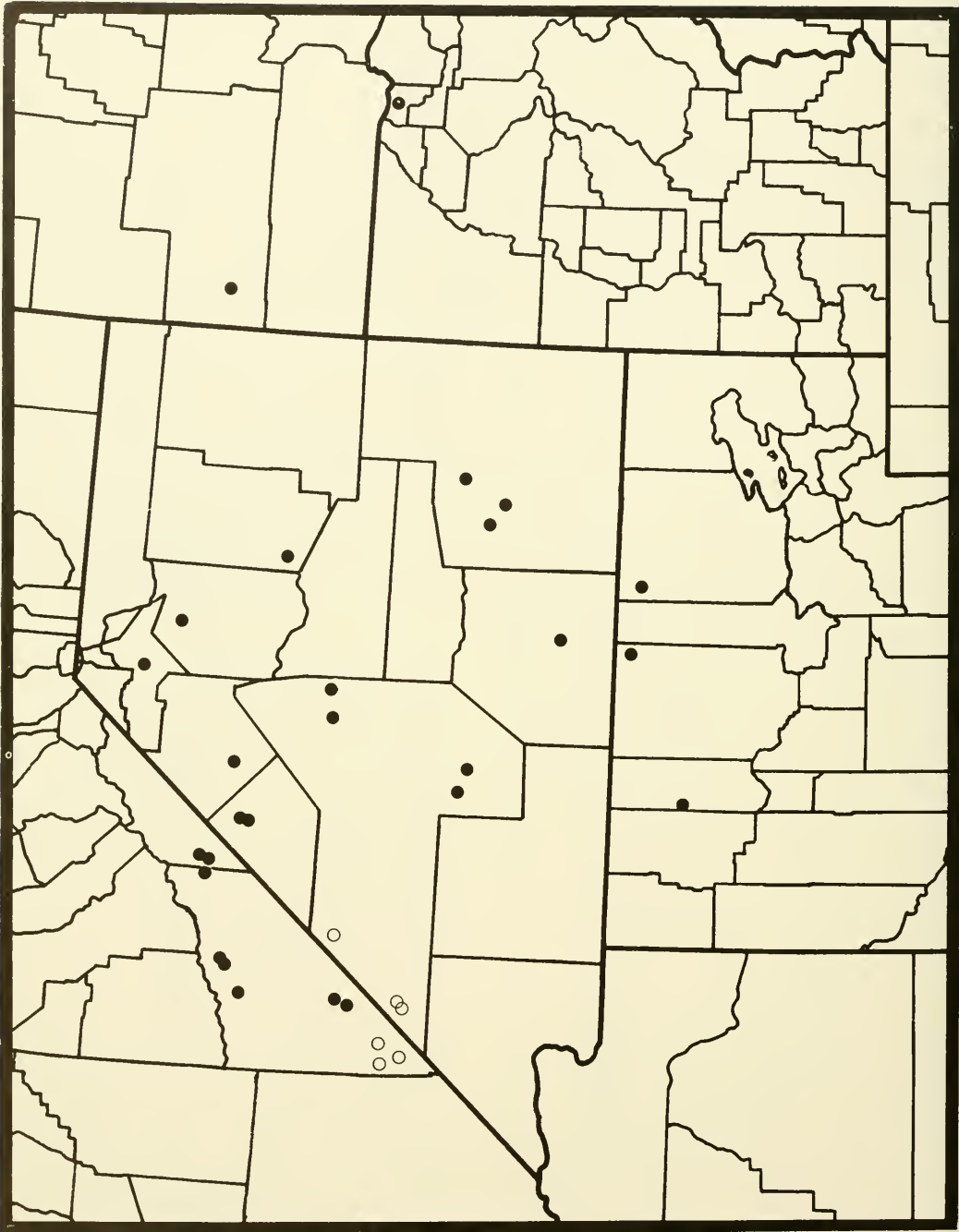


Fig. 2. Distribution of *Centaurium namophilum* var. *namophilum* (open circle) and var. *nevadense* (closed circle) in the western United States.

T.5S., R.33E., sec. 19, ca 4200 ft, 23 Jul 1976, *Reveal 4584* (MARY and 9 duplicates). IDAHO: County Unknown: Lewis' River (=Snake R.), 1834, *Nuttall s.n.* (BM, GH). Payette Co.: New Plymouth, 2200 ft, 1 Jul 1910, *MacBride 321* (UC). NEVADA: Churchill Co.: 6 mi N of Fallon, 6 Jul 1937, *Allen 284* (UC). Elko Co.: 0.2 mi W of Elko Poor Farm along Humboldt R., 9 Jun 1941, *Holmgren 1000* (UC); Ruby Valley, Sulphur Hot Springs, T.31N., R.59E., sec. 11, 6050 ft, 7 Jul 1969, *Holmgren & Kern 3663* (BRY, C, CAS, NY, RENO, WTU); Ruby Valley, 6000 ft, Aug 1865, *Watson 945* (GH); Ruby Valley, 12.9 mi SW of U.S. Hwy. 93 on Nev. Hwy 11, T.32N., R.60E., sec. 20, 31 Jul 1978, *Williams & Tiehm 78-267* (MARY); "Point," at edge of Ruby Lake Nat. Wildlife Ref., T.27N., R.58E., sec. 2, 18 Aug 1978, *Williams & Williams 78-318* (MARY). Esmeralda Co.: NE branch of Fish Lake Valley nr. Gap Springs, 5000 ft, 26 Sep 1938, *Archer 7251* (RENO, UC); nr. Gap Springs, T.1N., R.36E., sec. 5, 13 Aug 1978, *Reveal 4830* (MARY and 21 duplicates); Gap Springs, T.1N., R.36E., sec. 5, 13 Aug 1978, *Reveal 4831* (MARY and 23 duplicates); Gap Springs, T.1N., R.36E., sec. 5, 13 Aug 1978, *Reveal 4833* (MARY and 6 duplicates); Gap (Gap Springs?), 4000 ft, Jul 1886, *Shockley 531* (UC, W); Gap Springs, T.2N., R.36E., sec. 20, 3 Aug 1978, *Williams & Tiehm 78-301* (MARY). Lyon Co.: Wabuska Hot Springs, 0.5 mi N of Wabuska, T.15N., R.25E., sec. 16, 19 Aug 1978, *Broome 2375* (CAS and 23 duplicates); "boiling spring, Bent of Walker R." (=Wabuska Hot Spring), 1859, *H. Engelmann s.n.* (GH). Mineral Co.: Sodaville, 3 mi S of Mina along U.S. Hwy. 95, 22 Aug 1978, *Broome 2385* (CAS and 14 duplicates); Sodaville, 23 Aug 1978, *Broome 2386* (CAS and 4 duplicates); Sodaville, 4650 ft, 12 Aug 1978, *Reveal 4828* (MARY and 21 duplicates); Sodaville, 3 Aug 1978, *Williams & Tiehm 78-302* (MARY). Nye Co.: Smokey Valley, Darroughs Hot

Springs, T.11N., R.43E., sec. 7, 24 Jul 1978, *Goodrich 11909* and *11910* (MARY); Smokey Valley, T.14N., R.43E., sec. 34, 5450 ft, 7 Aug 1978, *Goodrich 12147* (MARY); Railroad Valley, Blue Eagle Spring, T.8N., R.57E., sec. 11, 4760 ft, 23 Jul 1980, *Tiehm & Williams 6193* (MARY); Hot Creek Springs, 8 mi WSW of Sunnyside, T.6N., R.61E., sec. 17, 5220 ft, 29 Aug 1980, *Welsh & Thorne 558* (MARY); Darroughs Hot Springs, T.11N., R.43E., sec. 29, 24 Jul 1978, *Williams & Williams 78-235* (MARY). Pershing Co.: Dixie Valley, Sou Hot Springs, T.26N., R.38E., sec. 29, 19 Jun 1978, *Broome et al. 2172* (CAS and 4 duplicates). White Pine Co.: Steptoe Valley, Monte Neva Hot Springs, T.21N., R.63E., sec. 24, 6050 ft, 28 Jun 1978, *Pinzl & Williams 1927* (MARY); Steptoe Valley, Monte Neva Hot Springs, T.21N., R.64E., sec. 22, 17 Jul 1979, *Thorne & Harrison 660* (BRY, MARY). OREGON: Harney Co.: shores of Borax (=Hot) Lake, T.37S., R.33E., sec. 14, 16 Aug 1978, *Broome 2366* (CAS and 15 duplicates); margin of Borax Lake, 28 Jun 1936, *Peck 19087* (WILLU, WTU). UTAH: Beaver Co.: Escalante Valley, 3 mi S of Thermo Siding, 14.5 mi WSW of Minersville, T.31S., R.12W., sec. 21, 5050 ft, 27 Aug 1980, *Welsh et al. 20136* (MARY); Millard Co.: 6.5 mi E of Gandy, S of Salt Marsh Lake, T.16S., R.18W., sec. 6, 4788 ft, 5 Sep 1976, *Welsh et al. 14512* (BRY). Tooele Co.: Six Mile Spring, 5 mi NW of Callao, T.10S., R.17W., sec. 9, 4800 ft, 20 Jul 1978, *Welsh et al. 17701* (BRY). County unknown: nr. Salt Lake City, 1901, *McVicker s.n.* (UC).

The new variety differs from var. *namophilum* (Reveal et al., 1974) chiefly in the more ascending, corymbose branching, and the smaller, darker rose pink corollas that are mostly less than 17 mm long, and by having styles shorter than or scarcely exceeding the stamens at anthesis. The following key will serve to differentiate the varieties most of the time.

- A. Principal leaves usually linear and sharply recurved; inflorescence a paniculate cyme with a definite central axis, the main branches diverging at a 45 degree or greater angle; ultimate peduncles generally shorter than the flowers and thus the flowers congested at tips of the branches; corolla pale to medium pink, the corolla-lobes equaling or more than half as long as corolla-tube, the stamens well exerted from the corolla-tube and these exceeded by the style *C. namophilum* var. *namophilum*

- AA. Principal leaves lanceolate or narrowly oblong, ascending or merely outcurved; inflorescence a diffuse corymbose cyme with the main branches ascending at less than a 45 degree angle from the axis; ultimate peduncles usually longer than the flowers and thus the flowers not appearing congested at tips of the branches; corolla medium to deep rose pink, the corolla-lobes less than half as long as corolla-tube, the stamens only slightly exerted from corolla-tube and equaling or exceeding the style *C. namophilum* var. *nevadense*

Centaurium namophilum var. *namophilum* is endemic to a narrow desert valley about 45 miles long situated between the Greenwater Mountains on the west and the Resting Spring Range on the east (Fig. 2). The plant occurs from the vicinity of Beatty (Ripley & Barneby 3994, CAS) in southern Nye Co., Nevada, southward along the Amargosa River drainage to near Tecopa, Inyo Co., California. The California collections of this variety (Coville & Funston 275, US, from Resting Springs Valley in 1891; Kerr s.n., CAS, UC, from Shoshone in 1934; and Roos & Roos 4927, RSA, UC, US, from Tecopa in 1950) represent populations that may no longer be extant. The variety could not be located in 1978 despite a careful search of these sites.

About 33 miles west and slightly north of the type locality of var. *namophilum* (in Ash Meadows, Nye Co., Nevada) and across the Funeral-Greenwater mountain system, is the Furnace Creek area in Death Valley, Inyo Co., California. This is now the site of the Death Valley Museum and visitor's center. *Centaurium* apparently exists no longer in this site, but was formerly collected at Furnace Creek in 1915 (S. B. Parish 10035, UC) and at nearby Texas Spring in 1935 (Gilman 1416, US). These collections quite closely resemble the plants from Shoshone and Tecopa referred above to var. *namophilum*. However, they are of the short-styled form with shorter corolla-lobes, and are considered, somewhat arbitrarily, to belong to var. *nevadense*. They more closely resemble the populations of var. *nevadense* that occur some 60 miles west in Owens Valley, at elevations of 3500 ft and above, and other populations scattered through Nevada and adjacent states (Fig. 2), than they do var. *namophilum*.

The var. *nevadense* is the same as *Erythraea nuttallii* sensu Gray (1876) and Coville (1893). Gray accurately distinguished *E. nuttallii* from *E. douglasii* A. Gray (a superfluous name for *Centaurium exaltatum*)

and gave its range as "Nevada, as near as Ruby Valley, and in adjacent parts of Idaho and Utah."

Erythraea nuttallii S. Wats. (1871a) was based on several different elements. Watson referred Nuttall's manuscript names "*E. longiflora*," "*E. elata*," and "*E. tenella*" to this species. However, plate 29 that accompanied the protologue clearly is based on a collection from Carson City, Nevada, gathered by Charles L. Anderson (29), and is the only specimen cited by Watson other than his own 945. Watson did refer to his own Nevada locations (Unionville, Huntington, and Ruby Valley). I have examined the Anderson collection (GH) and the Nuttall specimens upon which the three unpublished names were based (BM, GH, PH). The Anderson specimen is nearly identical to the published figure (t. 29), whereas none of the Nuttall material bears much resemblance to the plate, nor does Watson 945. The Anderson collection, however, is clearly representative of *Centaurium exaltatum*. Because it served as the model for the plate and is not excluded by Watson's description, Anderson 29 (GH!) is hereby designated the lectotype of *E. nuttallii*, and thus that name becomes a taxonomic synonym of *C. exaltatum*.

As for the three Nuttall names mentioned by Watson (1871a), the collections on which they were based represent three discordant elements. Nuttall's "*E. longiflora*" is *Centaurium namophilum* var. *nevadense*; his "*E. elata*" is typical *C. exaltatum*; and his "*E. tenella*" is *C. floribundum* (Benth.) B. L. Robinson. These specimens were gathered by Nuttall on a trip across the Rocky Mountains with Nathaniel J. Wyeth in 1834 (Graustein 1967). "*Erythraea longiflora*" and "*E. elata*" were gathered along the "Lewis' River, R. Mts.," which now refers to the Snake River of southern Idaho and Oregon. His specimen of "*E. tenella*" was gathered from "Port Neff, Columbia River," which is a reference to the

Portneuf River, a tributary of the Snake River in eastern Idaho. Nuttall and Wyeth were there for several weeks in July 1834 while Wyeth was constructing Fort Hall, a trading post along the Snake River near the mouth of the Portneuf (Robertson 1963). Unfortunately, there is no direct information as to where, along the Lewis' River, Nuttall may have gathered his specimens. Wyeth's party was along the Snake River only near Fort Hall and on the Idaho-Oregon border near the mouth of the Boise River where the party crossed into Malheur Co., Oregon, on 24 August. They stayed along the Snake River until reaching the Burnt River 27 August (McKelvey, 1955). Because both *C. exaltatum* and *C. namophilum* var. *nevadense* are known from western Idaho, it is possible Nuttall gathered his material in this area.

Asa Gray (1876) correctly excluded Nuttall's "*Erythraea tenella*" and "*E. elata*" from the concept of *Erythraea nuttallii*, leaving "*E. longiflora*," Anderson 29, a collection by Henry Engelmann (GH), and the Watson collection (Watson 945, GH) from Ruby Valley, Nevada. Unfortunately, only the Ruby Valley collection seems to be extant, and this is var. *nevadense*. It is the only location for the collection number cited by Watson (1871b) himself, and thus it is likely that the plants from Unionville and Huntington, Pershing Co., Nevada, either were not preserved or were incorporated all together into a single collection. As for the Engelmann collection, this too is var. *nevadense*, collected during the 1857-1859 wagon road survey of James Simpson (Jackson 1964) at Wabuska, Lyon Co., Nevada.

George Engelmann, the famed St. Louis botanist and brother of Henry (Reveal 1972), stated in 1878, "This plant [*Erythraea douglasii*] has been confounded by Mr. Watson with his *E. nuttallii*, which, however, is a smaller and more leafy plant, with larger flowers and much larger seeds (0.65 mm long), but much smaller stigmas." Still, Engelmann failed to lectotypify Watson's species, or to circumscribe it correctly.

The incomplete distinctions made in the past between *Centaurium namophilum* var. *nevadense* and *C. exaltatum* are understandable because, in a manner that is typical of sympatric species of *Centaurium*, these

two entities converge greatly when found together. It is sometimes with only the greatest of difficulty that poorly prepared herbarium material can be separated. The main characters by which *C. exaltatum* may be distinguished from var. *nevadense* are its broader, more elliptical leaves, the dichotomous (vs. trichotomous) peduncles, the paler pink or bluish, generally four-merous flowers, the shorter and more blunt corolla lobes, and the generally thicker, more included style and stigma.

ACKNOWLEDGMENT

I thank Cristalyn M. Cagle, Margaret J. Williams, and James L. Reveal for their help in field research, and Reveal for suggestions and review of the manuscript.

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ON THE TYPIFICATION OF *SALVIA DORRII* (LAMIACEAE)¹

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ABSTRACT.— The type of *Salvia dorrii* is shown to represent the Great Basin phase of the species (currently called subsp. *argentea*) rather than the Mojave Desert expression as implied by Epling and others. The Mojave Desert phase is hereby renamed *S. dorrii* var. *pilosa* (A. Gray) Strachan & Reveal.

In the Intermountain Region, three phases of *Salvia dorrii* (Kellogg) Abrams (Lamiaceae) are reported. The northern var. *carnosa* (Dougl. ex Greene) Cronq. of Washington and Oregon barely enters the Region along the Snake River on the Oregon-Idaho border. The widespread Great Basin plant has been called subsp. *argentea* (Rydb.) Munz, but the Mojave Desert element, long referred to as subsp. *dorrii*, was not considered to be in the Region even though the type was collected in west central Nevada. An examination of the variation in the *S. dorrii* complex throughout its range (by Strachan), and specifically that in the Intermountain Region (by Reveal), has shown some minor problems that can be resolved at this time.

When *Salvia dorrii* was originally proposed, it was placed in the genus *Audibertia* Benth. in Lindl., a homonym of *Audibertia* Benth., a synonym of *Mentha* L., and apparently was based on a C. Herbert Dorr collection supposedly gathered near Virginia City, Nevada (Epling 1938, Ewan 1967). This original collection has been lost (Epling 1938). Kellogg (1863) mentioned Dorr collections for three new species. Under *Lilium parvum* he thanked "Mr. C. H. Dorr for specimens from Nevada Territory." The type of *Viola aurea* was found by "Mr. C. W.[sic] Dorr from Nevada Territory," but in his description of *Spraguea paniculata* Kellogg wrote that the type was found by Dorr "in a ravine extending to the west, about six miles from Virginia City, Nevada Territory, at an altitude of 3,000 feet." It was this latter informa-

tion that probably led to the assumption that the type of *A. dorrii* came from near Virginia City. In his description of *A. dorrii*, Kellogg gives no indication at all as to the collector or the place of collection. The specific epithet is our only link with Dorr.

Interestingly, there is a series of subsequent species found in western Nevada and along the eastern slope of the Sierra Nevada in California proposed by Kellogg (1863) without any reference to collector or exact location (except one). These are *Lupinus confertus* (p. 192), *L. calcaratus* (p. 195), *L. caudatus* (p. 197), *Oenothera nevadensis* (p. 224—his next paper), *O. cruciformis* (p. 227), and *Viola chrysantha* var. *nevadensis* (p. 229). Only *O. cruciformis* has a location cited for it, this being "Steamboat Springs, Nevada Territory." Raven (1962) did not find a type specimen of *O. cruciformis* and proposed a neotype for this narrowly endemic species. Only a fragment of a specimen, without any information, was found for *O. nevadensis* (Raven 1969). This specimen was taken by Raven to represent Kellogg's original material. As for the three lupines, we can find recently published information on two. Hess and Dunn (1970) cite a Carson Valley collection of Kellogg's as the type of *L. caudatus*. Although Greene (1887) indicated that Kellogg did some collecting and illustrating of plants, both Ewan (1955) and Greene insist that Kellogg did not begin active botanizing until his Alaskan trip in 1867. Neither Reifschneider (1964) nor Ewan (1967) report Kellogg as a Nevada collector. There is no indication on

¹Supported, in part, by National Science Foundation Grant BMS75-13063 (Reveal). This is Scientific Article A2991, Contribution No. 6053 of the Maryland Agricultural Experiment Station, Department of Botany.

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the specimen of *L. caudatus*, now deposited at the California Academy of Sciences, when it was collected or who made the collection. According to Curran (1885), this species was originally gathered by Dorr near Virginia City, but she gives no evidence to support this conclusion. It is probable that Kellogg was not the collector of this specimen as suggested by Hess and Dunn. It should be noted that John Allen Veatch, an associate of Kellogg's then living in Virginia City, did collect in Carson Valley. We suggest that the lupine could just as well have been gathered by Veatch as it may have been gathered by Dorr.

Dunn (1957) reports no type specimen for *L. calcaratus*, but Curran (1885) states the plant was collected "by H. C. [sic] Dorr, near Virginia City," indicating that perhaps a specimen must have been extant at one time, although it is possible she just assumed it was gathered by Dorr near Virginia City. Day (pers. comm.) says there is no type for *L. confertus*, and Cox (1972) suggests the need for a neotype. As for the *Viola*, no specimen is extant (Day, pers. comm.), and there is some question as to the exact meaning of the name "nevadensis." J. T. Howell and A. Day (pers. comm.) have called to our attention that *V. douglasii* (as *V. chrysantha* is now called) is a Sierra Nevada species, and is not found in the state of Nevada. Perhaps the plant came from the mountains of California rather than Nevada. We cannot tell. Curran (1885), in her review of the early names proposed by Kellogg, states the variant was hardly different from typical *V. douglasii*, but there is no indication that she actually saw a specimen.

In reviewing the distribution of the plants attributed to Dorr, two occur in the Virginia City area of west central Nevada. These are *Viola aurea* and *Spraguea umbellata* Torr., the correct name for *S. paniculata*. However, we have no record of *Lilium parvum* from the Intermountain Region of Nevada (Cronquist et al. 1977), although it is found on the eastern slope of the Sierra Nevada in Nevada. We now suspect that Dorr collected several specimens that were used by Kellogg to propose new species. For unknown reasons Kellogg failed to record who made the collections. One possible reason is that Kellogg was unable to retain Dorr's specimens for the

California Academy of Sciences' collection and decided not to cite them. We have found no Dorr or Kellogg specimen of *S. dorrii* among the several hundred specimens we have observed of the complex, and, thus, we too must conclude that the type is lost.

The only indication as to the original intent of the type is that represented by the illustration published by Kellogg (1863). Epling (1938) referred *Audibertia dorrii* to synonymy under his *Salvia carnosa* Dougl. ex Greene subsp. *pilosa* (A. Gray) Epling without comment, although his range map specifically excluded the Virginia City area of western Nevada. The Kellogg illustration is not critical enough to fully distinguish his species from either the Great Basin phase, subsp. *argentea*, or the Mojave Desert plant, subsp. *dorrii*, which would later (Abrams 1951) include what Epling termed *S. carnosa* subsp. *pilosa*. The Kellogg illustration shows a rather congested inflorescence. This is similar to the condition found in the Mojave Desert phase. The short hairs on the ciliated bracts, however, are more similar to what is found on the bracts of the Great Basin phase. In reading the description additional characters can be noted. The verticillasters are given as "proliferous or condensed whorls, the whorls often remote or separated, of about three or more." The bracts are stated to be "externally somewhat strigose," a distinctive feature that clearly indicates the original material was not the southern phase characterized by long, pilose hairs on the bracts. Finally, an examination of other collections from the Virginia City area reveal only plants of "subsp. *argentea*." We believe the epithet *dorrii*, which must be typified with the Kellogg illustration according to Art. 9.3 of the International Code (Stafleu et al. 1978), applies to the Great Basin phase of the species rather than the southern desert expression as proposed by Epling and followed by Abrams (1951), Munz and Keck (1959), and others.

As a result, we propose to place *Audibertia argentea* Rydb. in synonymy under *Salvia dorrii* var. *dorrii*, and recognize *S. dorrii* var. *pilosa* (A. Gray) Strachan & Reveal, comb. nov., based on *Audibertia incana* var. *pilosa* A. Gray, Syn. Fl. N. Amer. ed. 2, 2(1): 461. 1886 as typified by Parish & Parish 1309.

Actually, var. *pilosa* is found in the Great Basin. Specimens have been found in the Lahontan Basin system of central and northern Washoe County and the Black Rock Desert area of Humboldt County, Nevada, westward into eastern Lassen County, California. These isolated populations differ from the southern plants in having narrower bracts and somewhat shorter, but still pilose hairs on the outer surface and margin of the bracts. The typical form of var. *pilosa* is found as far north as the northern end of Owens Valley in extreme southern Mono County, California.

Additional variation is known to exist in *Salvia dorrii* as now defined. As these variants are found outside the boundaries of the Inter-mountain Region, they will be discussed later.

ACKNOWLEDGMENT

We thank the many curators who have sent us material for study, Alva Day and John Thomas Howell (CAS) for their assistance with critical Kellogg types, and Barbara J. Ertter for comments.

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PARASITES OF INDOCHINESE REFUGEES ENTERING UTAH COUNTY, UTAH: A TWO-YEAR SURVEY

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ABSTRACT.— A survey of parasites from 39 stool specimens taken from 36 Indochinese refugees who are now living in Utah County, Utah, indicated representative intestinal helminths (worms), and protozoans upon clinical examination. Approximately 75% of the stools contained nematodes, and 55.5% had protozoans. Parasites found were *Entamoeba coli*, *Chilomastix mesnili*, *Endolimax nana*, *Giardia lamblia*, *Iodamoeba buetschlii*, *Clonorchis sinensis*, *Trichuris trichiura*, *Ascaris lumbricoides*, and *Plasmodium vivax*. The most common protozoan observed was *Entamoeba coli* (1979 and 1980) while the most common helminths were *Ascaris lumbricoides* (1979) and *Clonorchis sinensis* (1980). These data were comparable to studies of refugees at two other laboratories in Utah and one at Washington, D.C.

Since May 1975, approximately 150,000 Indochinese refugees have entered the United States, a small percent of whom now live in Utah. More are expected. A majority of the refugees arrive directly from camps in Malaysia, Indonesia, Thailand, etc., with only preliminary screening for tuberculosis, leprosy, venereal disease, and mental defects and disorders, which is done by the Center for Disease Control (CDC) of the United States Public Health Service [Morbidity and Mortality Weekly Report (MMWR) 1979]. According to the cited article, the CDC does not consider it necessary to routinely screen all Indochinese refugees for intestinal or blood parasites. This is not regarded by the CDC as being critical because adequate sewage disposal and improved hygienic practices maintained in the USA will decrease the risk posed by intestinal helminths and protozoa by interrupting life cycles and minimizing direct fecal contamination. The possibility of malaria transmission is small, especially in the winter months, due to the limited number of anopheline mosquitoes in Utah.

In 1979 President Carter announced that 14,000 Indochinese refugees would be accepted monthly for resettlement in the United States. The CDC at Atlanta, Georgia, is responsible for the medical screening of refugees while they are still abroad and for the inspection of refugees upon arrival at USA ports of entry.

United States Public Health Service teams have recently visited areas in California, Oregon, Washington, and Hawaii that have already received large numbers of refugees, as well as refugee camps and embarkation areas in Southeast Asian countries. From these visits, as well as from limited surveillance data and the experience gained in the resettlement of over 150,000 Vietnamese refugees in the United States since May 1975, the following may be expected:

1. "The majority of refugees will be free of major contagious diseases;
2. Where an illness is present, it will likely represent a personal rather than a public health problem; and
3. The main health problems, perhaps exceeded only by the stress of resettlement itself, will include tuberculosis and parasitic diseases" (MMWR 1979).

The CDC continues to survey resettlement areas in the U.S. for parasitic diseases. One survey in Illinois (February 1979) found hookworms to be the most common intestinal parasite in the group (64 percent), followed by *Giardia lamblia* (18 percent), *Trichuris* (12 percent), and *Ascaris* (9 percent) (MMWR 1979). The purpose of our investigation was to determine the presence of intestinal and blood parasite infections of refugees in Utah County, Utah, by performing direct examinations of blood and fecal samples and to

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compare these data with results for other areas in Utah and for Washington, D.C.

MATERIALS AND METHODS

During 1979, a series of fecal samples taken three times weekly were obtained from each patient in plastic specimen cups into which 60 ml of 10 percent formalin was added for preservation. The sampling was varied in 1980 in that specimens were obtained from the Utah County Public Health Office following visits by refugees. Samples were then stored in a refrigerator at 5 C for 1 to 36 hours until concentration and staining procedures were performed. Samples were concentrated by the formalin-ether concentration technique (Richie 1948), and preliminary examinations were made by mixing one drop of fecal concentrate with one drop iodine, covering with a coverslip and examining under various powers with a microscope. Permanent slides were prepared with the trichrome stain technique (Garcia and Ash 1979) and iron hematoxylin stain technique (Spencer and Monroe 1975). The zinc flotation helminth egg isolation technique (Spencer and Monroe 1975) was also used on several samples.

Blood samples were drawn from a median cubital puncture into heparinized vacutubes from the majority of the patients. A finger prick was used for some, with the blood being collected in a heparinized capillary tube, care being taken not to "milk" the tissue to avoid diluting the blood with interstitial tissue fluid. From these blood samples, thick and thin smears were prepared from the Giemsa stain technique (Shute 1966, Shute and Maryon 1966) and examined microscopically.

RESULTS

Examination of fecal samples from 6 refugees in 1979 (Table 1a) and 30 refugees in 1980 (Table 1b) revealed the presence of five protozoan parasites (*Entamoeba coli*, *Chilomastix mesnili*, *Endolimax nana*, *Iodamoeba buetschlii*, and *Giardia lamblia*) and five helminth parasites (*Ascaris lumbricoides*, *Trichuris trichiura*, hookworms, *Clonorchis sinensis*, *Strongyloides stercoralis*) (larvae) (Tables 2a and 2b). Of the helminths observed four were roundworms and one (*C. sinensis*) was a fluke. Thick and thin blood smears from 66 percent (2/3) of the 1979 refugees and 48 percent (11/23) of the 1980 group were positive for malaria (*Plasmodium vivax*) (Table 3).

For the 1979 sample, one of the two refugees from whom both blood and fecal samples were taken was found to be free of pathogenic parasites, but the other had both blood and intestinal infections. One of the three refugees who gave stool samples was found to have a multiple infection, another an infection by a single pathogenic species, and the third was found to be pathogen-free. One Indochinese refugee, who submitted blood only, was found to harbor malarial parasites.

Data from the stool and blood samples examined during 1980 included individuals with no parasite infections and those with intestinal parasites, blood parasites, or both. Four refugees had four different species of intestinal parasites. The combined results of 1979 and 1980 show a high incidence of parasitism among the refugees entering Utah County. There were variations in percent infections for the two years, which would be expected due to the limited number of

TABLE 1a. Status for 6 of the 9 refugees checked in Utah County, Utah, for parasites, 1979.

Patient No.	Age	Sex	Height	Weight	Time in U.S.	Place of origin	Refugee camp	Time in camp
1	19	M	5'5"	102 lbs.	6½ months	Saigon	Malaysia	7 months
2	11	M	4'6"	70 lbs.	3 weeks	Saigon	Indonesia	8 months
3	54	M	5'5"	100 lbs.	3 weeks	Saigon	Indonesia	8 months
4	14	M	5'2"	90 lbs.	6½ months	Saigon	Malaysia	7 months
5	20	M	5'9"	110 lbs.	5 months	Saigon	Malaysia	8 months
6	17	F	5'2"	110 lbs.	6½ months	Saigon	Malaysia	7 months

TABLE 1b. Status for 28 of the 30 refugees checked in Utah County, Utah, for parasites, 1980.

Patient No.	Age	Sex	Arrival date, Utah Day/Month/Year	Refugee camp	Origin	Blood sample	Fecal sample
1	37	M	28-II-80	Chieng Khong, Thailand	Laos	1	0
2	16	M	28-II-80	Chieng Khong, Thailand	Laos	1	0
3	14	M	28-II-80	Chieng Khong, Thailand	Laos	1	0
4	7	F	28-II-80	Chieng Khong, Thailand	Laos	1	0
5	10	M	28-II-80	Chieng Khong, Thailand	Laos	1	0
6	5	M	28-II-80	Chieng Khong, Thailand	Laos	1	0
7	34	F	28-II-80	Chieng Khong, Thailand	Laos	1	0
8	55	M	1-III-80	Ubon, Thailand	Laos	1	1
9	50	F	1-III-80	Ubon, Thailand	Laos	1	1
10	29	M	1-III-80	Ubon, Thailand	Laos	1	1
11	19	M	1-III-80	Ubon, Thailand	Laos	1	1
12	12	M	1-III-80	Ubon, Thailand	Laos	1	1
13	21	M	1-III-80	Ubon, Thailand	Laos	1	1
14	9	M	1-III-80	Ubon, Thailand	Laos	1	1
15	13	M	1-III-80	Ubon, Thailand	Laos	1	1
16	17	F	1-III-80	Ubon, Thailand	Laos	1	1
17	26	F	1-III-80	Ubon, Thailand	Laos	1	1
18	28	M	1-III-80	Ubon, Thailand	Laos	1	1
19	71	F	1-III-80	Ubon, Thailand	Laos	1	1
20	42	F	14-III-80	Nong Khai, Thailand	Laos	1	1
21	47	M	14-III-80	Nong Khai, Thailand	Laos	1	1
22	4	F	14-III-80	Nong Khai, Thailand	Laos	1	1
23	20	M	14-III-80	Nong Khai, Thailand	Laos	0	1
24	7	M	14-III-80	Nong Khai, Thailand	Laos	0	1
25	18	M	14-III-80	Nong Khai, Thailand	Laos	0	1
26	12	M	14-III-80	Nong Khai, Thailand	Laos	0	1
27	9	M	14-III-80	Nong Khai, Thailand	Laos	0	1
28	28	M	12-VIII-80	Nong Khai, Thailand	Laos	1	0

TABLE 2a. Results of 9 stool specimens examined from 6 refugees entering Utah County (1979).

Parasite	No. of infected stools	% Infected stools
<i>Entamoeba coli</i>	2	22
<i>Chilomastix mesnili</i>	1	11
<i>Endolimax nana</i>	1	11
<i>Giardia lamblia</i>	1	11
<i>Entamoeba histolytica</i>	0	0
Hookworms	0	0
<i>Ascaris lumbricoides</i>	5	56
<i>Trichuris trichiura</i>	2	22

samples in 1979. For both years *Entamoeba coli*, a commensal, was the common protozoan parasite (22 percent, 37 percent) followed by *Giardia lamblia*, an intestinal parasite (11 percent, 10 percent) Table 2a, 2b. The most common intestinal parasite for 1979 was *Ascaris lumbricoides* (60 percent) followed by *Trichuris trichiura* (20 percent). For 1980 the fluke *Clonorchis sinensis* was first (40 percent), followed by *Trichuris trichiura* (23 percent), hookworms (*Necator americanus*

TABLE 2b. Results of 30 stool specimens examined from 30 refugees entering Utah County (1980).

Parasite	No. of infected stools	% Infected stools
<i>Entamoeba coli</i>	11	37
<i>Chilomastix mesnili</i>	1	3
<i>Endolimax nana</i>	0	0
<i>Giardia lamblia</i>	3	10
<i>Entamoeba histolytica</i>	0	0
<i>Iodamoeba buetschlii</i>	4	13
Hookworms	6	20
<i>Clonorchis sinensis</i>	12	40
<i>Trichuris trichiura</i>	7	23
<i>Ascaris lumbricoides</i>	4	13
<i>Strongyloides stercoralis</i> (larvae)	1	3

or *Ancylostoma duodenale*) (27 percent), and *Ascaris lumbricoides* (14 percent). For both years the only blood parasite encountered was *Plasmodium vivax* (malaria).

Fertilized helminth eggs of *Ascaris lumbricoides* and *Trichuris trichiura* were present both years, as well as unfertilized *Ascaris lumbricoides* eggs. There were no cestode

TABLE 3. Blood parasites (*Plasmodium vivax*) observed from refugees entering Utah County, 1979 and 1980.

Year	No. of samples	No. with parasites	% Infected
1979	4	3	75
1980	23	11	48

eggs in any of the fecal specimens. The nematodes or roundworms were the most common group of endoparasites.

The protozoan parasites were found in both cyst and trophozoite stages. *Entamoeba*

coli was only found in the trophozoite stage, and *Chilomaxtis mesnili*, *Endolimax nana*, and *Giardia lamblia* were observed only in the cyst stage. *Plasmodium vivax* was the blood parasite found in some of the blood samples (Table 3).

Data from the samples we checked were compared with results from concurrent parasite studies of refugees in Salt Lake and Utah Counties, Utah, and Washington, D.C. (Tables 4,5,6).

DISCUSSION

Although more than 100,000 Indochinese refugees have been admitted to the United

TABLE 4a. Intestinal parasitism in Indochinese refugees, by age group, Salt Lake County, Utah, July-December 1979 (MMWR 1979).

	Age 0-4	Age 5-15	Age 16-24	Age 25-44	Age 45	All ages
Number examined	38	98	93	98	29	356
Helminths						
<i>Ascaris lumbricoides</i>	4 (11)*	7 (7)	7 (8)	5 (5)	1 (3)	44 (12)
<i>Clonorchis sinensis</i>	0	0	5 (5)	1 (1)	0	6 (2)
Hookworms	1 (3)	4 (4)	10 (11)	8 (8)	2 (7)	25 (7)
<i>Strongyloides stercoralis</i>	2 (5)	0	0	0	0	2 (1)
<i>Trichuris trichiura</i>	0	6 (6)	8 (9)	16 (16)	1 (3)	31 (9)
Protozoans						
<i>Endolimax nana</i>	0	5 (5)	5 (5)	1 (1)	2 (7)	13 (4)
<i>Entamoeba coli</i>	0	4 (4)	2 (2)	7 (7)	0	13 (4)
<i>Entamoeba histolytica</i>	0	0	2 (2)	0	1 (3)	3 (1)
<i>Giardia lamblia</i>	3 (8)	6 (6)	6 (6)	1 (1)	0	16 (4)

*Number of persons infected (percent infected).

TABLE 4b. Intestinal parasites in Indochinese refugees, by age group, Utah County, Utah, 1980.

	Age 0-4	Age 5-15	Age 16-24	Age 25-44	Age 45	All ages**
Number examined	53	120	102	170	49	494
Helminths						
<i>Ascaris lumbricoides</i>	6 (12)*	26 (22)	17 (17)	19 (11)	6 (12)	74 (15)
<i>Clonorchis sinensis</i>	7 (13)	38 (32)	31 (31)	42 (25)	6 (12)	124 (25)
Hookworms	11 (21)	40 (34)	25 (25)	40 (24)	18 (37)	134 (27)
<i>Strongyloides stercoralis</i> (larvae)	1 (2)	5 (4)	3 (3)	3 (2)	2 (4)	14 (3)
<i>Trichuris trichiura</i>	7 (13)	34 (28)	16 (16)	20 (12)	9 (18)	86 (18)
<i>Taenia</i> sp.	0	3 (3)	3 (3)	1 (1)	0	7 (1)
Protozoans						
<i>Endolimax nana</i>	1 (2)	6 (5)	4 (4)	6 (4)	3 (6)	19 (4)
<i>Entamoeba coli</i>	8 (15)	17 (14)	12 (12)	13 (8)	6 (12)	56 (11)
<i>Entamoeba histolytica</i>	1 (2)	7 (6)	2 (2)	6 (4)	2 (4)	18 (4)
<i>Giardia lamblia</i>	7 (13)	18 (15)	15 (15)	12 (7)	2 (4)	54 (11)
<i>Entamoeba hartmani</i>	1 (2)	2 (2)	2 (2)	1 (1)	1 (2)	7 (2)

*Percent infection in parentheses

**254 males; 35 percent infected

240 females; 30 percent infected

States in the past year, very few population-based data have been published on their health conditions other than intestinal parasitism and tuberculosis (MMWR 1979). Representative data are essential for realistic planning of initial health-care delivery for this population. Health departments, clinics, or other agencies that have collected or are collecting data on the health status of representative samples of the arriving refugee population (not simply clinic samples of the ill) are encouraged to share their findings with local and state health departments and CDC (MMWR 1979).

Investigations of parasite incidence among incoming refugees show generally the same organisms being encountered, but not necessarily in the same proportion. This is evident with malaria. A CDC report concerning the health status of Vietnamese refugees arriving in the U.S. (MMWR 1975:158) reported that, of 77,526 refugees seen, only two cases of malaria were reported. More recent reports indicate a higher incidence of malaria, however, with malaria being the number one cause of death among the Cambodian

refugees in Thailand, followed by malnutrition (MMWR 28:545-546, 1979; MMWR 28:388-398, 1979). A random survey of one camp revealed *P. falciparum* malaria in 30 of 80 people (38 percent) screened (MMWR 28:545-546, 1979).

Malaria (*Plasmodium*) can be definitively diagnosed only through the careful microscopic examination of blood films. For our study, both thick and thin blood films were made and the slides were stained with the Giemsa stain.

The films were carefully dried, then examined with oil immersion for any malarial stage. The number of malarial stages per 100 red blood cells (RBC) was noted on all thick film slides.

A national comparison from CDC states that, as of 18 August 1979, there were 19 new cases of malaria reported, with a cumulative total of 408. In September of 1979, 10 new cases were reported, with a cumulative total of 519 (MMRW 1979).

TABLE 5a. Parasites of 13 refugees checked by the Utah County Public Health Department, 1979.

Parasite	No. infected refugees	% Infected
<i>Entamoeba coli</i>	4	31
<i>Entamoeba histolytica</i>	1	7
<i>Endolimax nana</i>	1	7
<i>Chilomastix mesnili</i>	1	7
<i>Giardia lamblia</i>	2	15
Hookworms	11	85
<i>Strongyloides stercoralis</i> (larvae)	2	23
<i>Ascaris lumbricoides</i>	4	31
<i>Trichuris trichiura</i>	1	7

TABLE 5b. Parasites of 494 refugees checked by the Utah County Public Health Department, 1980.

Parasite	No. infected refugees	% Infected
<i>Entamoeba coli</i>	48	8
<i>Entamoeba histolytica</i>	18	4
<i>Entamoeba hartmani</i>	9	2
<i>Endolimax nana</i>	21	5
<i>Chilomastix mesnili</i>	0	0
<i>Giardia lamblia</i>	52	11
Hookworms	132	27
<i>Strongyloides stercoralis</i> (larvae)	12	3
<i>Ascaris lumbricoides</i>	68	14
<i>Trichuris trichiura</i>	88	18
<i>Clonorchis sinensis</i>	125	26
<i>Taenia</i> sp.	5	1

TABLE 6. Intestinal parasitism in Indochinese refugee children, by age group, Washington, D.C., September-November 1979 (MMWR 1979).

	Age 0-4	Age 5-9	Age 10-18	All ages
Number examined	6	16	9	31
<i>Ascaris lumbricoides</i>	2 (33)*	9 (56)	3 (33)	14 (45)
<i>Clonorchis sinensis</i>	0	0	1 (11)	1 (3)
<i>Giardia lamblia</i>	1 (17)	4 (25)	1 (11)	6 (19)
<i>Hymenolepis nana</i>	0	1 (6)	1 (11)	2 (6)
<i>Strongyloides stercoralis</i>	0	2 (13)	3 (33)	6 (16)
<i>Trichuris trichiura</i>	0	3 (19)	0	3 (10)

*Number positive (percent positive).
All *Strongyloides* infections were in children from one family.

In a typical three-month period in Utah (1979), the Utah Bureau of Laboratories examined approximately 800 stool specimens, of which 76 (9.5 percent) were positive, with *Giardia lamblia* being the most commonly identified organism (4.8 percent), followed by *Trichuris* (0.5 percent), *Entamoeba histolytica* (0.13 percent), *Ascaris* (0.13 percent), and hookworms (0.13 percent) (Olsen and Fukushima 1977). Refugee screening is an efficient means of gaining information about parasites.

Giardia lamblia, *Chilomastix mesnili*, *Entamoeba coli*, and *Endolimax nana* are relatively nonpathogenic intestinal protozoans with a worldwide geographic distribution. They occupy different locations in the intestinal tract of humans, being asymptomatic or causing mild diarrhea (Spencer and Monroe 1977). The infective stage is the cyst that is passed out of the intestine with fecal material. Studies of these protozoans have shown that water can be contaminated with host fecal material.

Refugees infected with intestinal helminths and protozoa should not create a problem to the public. Adequate sewage disposal interrupts the transmission of the helminths, which require several days of incubation in soil to become infective.

In conclusion, because of present sanitary conditions in Utah County, no serious problems should occur due to refugees in this area. Further investigation, as well as host treatment and follow up of diagnosed cases, would be appropriate.

ACKNOWLEDGMENTS

The following students in Brigham Young University parasitology classes helped on this project: Eric T. Garner, Rory R. Gile, Donn A. Grimes, Dawn E. Kersey, Mary J. Rench, and Sterling R. Wadley.

Thanks to Dr. A. Flinders and others in the Utah County Health Department for providing data and support.

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THE INVERTEBRATE FAUNA OF THE CAVES OF THE UINTA MOUNTAINS, NORTHEASTERN UTAH

Stewart B. Peck¹

ABSTRACT.— Seven large caves in the Uinta Mountains, Utah, were surveyed for their invertebrate faunas. Thirty-eight species were found, and 30 of these are typical cave inhabitants. Diptera are the predominant group. Cave-restricted species are an amphipod, two diplurans, and possibly a *Rhagidia* mite. The caves were probably uninhabitable in the past glacial because of severe periglacial environmental conditions, and the faunas have moved into the present cave sites since deglaciation of the Uintas.

Since the helpful checklist of Nicholas (1960), much additional survey work has been completed on the cavernicolous invertebrate faunas of the United States (see review in Peck and Lewis 1978). However, gaps still exist in certain western states, and these should be filled in an attempt to achieve a comprehensive understanding and a unified general theory of the evolution and distribution of North American cave invertebrates (Peck 1978, 1981).

The Uinta Mountains of northeastern Utah are ringed by limestone and contain many caves, but no effort seems to have been made to characterize their fauna. Field work was conducted in August 1979 to remedy this.

Extensive information is available on the caves of Utah, although much of it exists in obscure publications. A general overview of Utah speleology is given by Green (1963a), and White (1979) discusses karst landforms in the Uinta Mountains. Brief information on the caves studied follows. These are the largest known in the Uintas and are the most likely to have a variety of microhabitats, and thus to support the greatest diversity of invertebrate fauna.

Cave locations are shown in Figure 1. They are indicated on USGS topographic maps and on U.S. Forest Service maps of the Ashley and Uinta Forests. All the caves are formed in the Madison and Deseret lime-

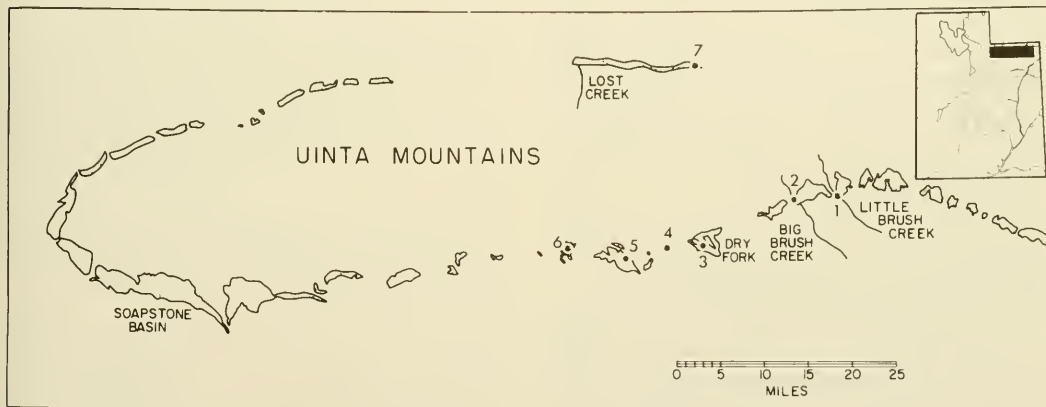


Fig. 1. Pattern of outcrop of Mississippian limestones ringing the Uinta Mountain uplift (adapted from White 1979). Caves surveyed for invertebrate faunas are: 1, Little Brush Creek Cave; 2, Big Brush Creek Cave; 3, Dry Fork Cave; 4, Ice Cave; 5, White Rocks Cave; 6, Pole Creek Cave; 7, Sheep Creek Cave. Inset shows location of Uinta Mountains in Utah.

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stones of Mississippian age. Because caves are fragile environments, excessive and careless visitation to them should not be encouraged.

Big Brush Creek Cave, Uintah County, Sec. 29, T 1 S, R 21 E, on Red Cloud Loop forest road 018, about 9000 ft elev., about 17 mi N of Vernal.

This cave lies in a large stream sink and has a very large entrance arch. Up and to the left of the entrance is an upper and irregular series of passages called the ice cave section. The main passage narrows somewhat before entering a huge room containing much wood debris, indicating that this and deeper areas of the cave fill completely with flood waters. The cave continues down through a series of crawls and chambers into a maze of water-scoured passages with pools. At 26,000 ft in length, and an 800 ft depth (White 1978, Green 1963b), it is the largest cave in Utah. Temperatures were 1 C in the first big room, and 6 C in the second (RH 93 percent).

Little Brush Creek Cave, Uintah County, Sec. 25, T 1 S, R 21 E, about 8000 ft elev., near route 44, about 18 mi N of Vernal.

The cave has a large arched entrance in a large sink into which flows a wet weather stream. In time of flood, water ponds in the sink and log jams occur in narrow passages. The cave is 15,000 ft long and 500 ft deep (White 1979, Green 1963a, 1963c). Fauna was found on rotting wood, flood debris, and sand. The temperature was 10 C (RH 88 percent). The local environment is boreal forest, with the north-facing hillside above the cave covered by spruce and fir.

Dry Fork Cave, Uintah County, Sec. 21, T 3 S, R 19 E, in Dry Fork Canyon, at about 8000 ft elev., about 18 mi NW of Vernal.

The entrance is a stoopway in a rock outcrop on a hillside. The cave is an ascending walking-crawling passage with about 100 ft of main passage (Green 1957), which is mostly dry but with some moist and wet areas. The cave floor is of dust, clay, sand, and small to large, rounded stream boulders. The temperature was 9 C (RH 94 percent). The sparse fauna was concentrated near moist areas and at moist *Neotoma* packrat droppings and decaying nest debris.

Ice Cave, Uintah County, Sec. 5, T 2 W, R 1 E, near the top of Ice Cave Peak, off forest

road 104, about 9700 ft elev., about 15 mi NNW of Lapoint.

The cave's slotlike entrance is at the bottom of an aspen-lined sink. The cave consists solely of a low chamber 30 feet wide and 60 feet long, floored with dirt and much ice. The fauna is concentrated on the cave ceiling and uses the cave as a daytime retreat or as an aestivation site. When insects die they fall to the ice and may be preserved there. Other arthropods are in litter and decaying debris at the base of the entrance slope. The air temperature was 4 C (RH 85 percent) 3 ft above the ice.

Whiterocks Cave, Duchesne County, Sec. 1, T 2 N, R 1 W, about 8000 ft elev., high on cliffs above Whiterocks River Canyon, about 10 mi N of Whiterocks, or 15 mi NNW of Lapoint.

The gated cave entrance is reached by an arduous climb. Entry is allowed only with forestry personnel and arrangements must be made with the Vernal office several weeks in advance. This is a large cave of irregular dimensions, and it is certainly in need of protection to conserve it. Much of this cave, about 3000 ft long, is generally moist but lifeless, and fauna was found associated with moist rat dung only near the entrance. Many dripstone pools are present but are also barren of life. The temperature was 7.5 C (RH 94 percent). The abundant packrat middens may contain a valuable record of past climatic and floristic changes in the area of the cave (see Van Devender and Spaulding 1979).

Pole Creek Cave, Duchesne County, Sec. 24, T 3 N, R 2 W, off forest road 117, around 7000 ft elev., about 12 mi NW of Whiterocks or 23 mi NNW of Roosevelt.

The cave entrance is a flood-water stream resurgence at the base of a limestone slope. The sink of Pole Creek is a broad area about ½ mi north. The low entrance leads to a large ascending stream passage floored with sand, mud, and water-sculptured rock. About 600 ft of passage exists before a deep pool floods the cave from wall to wall. The air temperature was 8.5 C (RH 87 percent) and the water was 8 C. The fauna was on damp soil near scarce bits of organic debris, or on the ceiling at the entrance.

Sheep Creek Cave, Daggett County, Sec. 16, T 2 N, R 19 E, at 7040 ft elev., about 7 mi SW of Manila.

The cave is formed in vertical limestones on the west wall of Sheep Creek Canyon where this intersects the Uinta Crest fault. The Forest Service has protected the cave entrance, some 30 m above the cave stream resurgence, by a gate, but this has been vandalized. The main cave passage is the abandoned upper level of the stream that now resurges at a lower level. I judge the ashy nature of much of the cave floor, the "burnt" smell in the cave, and the soot-darkened ceiling to indicate that large accumulations of organic matter, such as packrat nests, formerly existed here but have been burned. This likely happened in or before 1950, and is regrettable because a valuable paleoenvironmental record (see Van Devender and Spaulding 1979) has been mostly lost. A few isolated middens still exist near the entrance. The "burned" part of the cave is barren. Lower levels near the stream had a sparse fauna on mud banks. The stream seems to carry only finely divided organic matter. The air temperature was 9.5 C (RH 94 percent) at the stream and the stream was 9 C.

ANNOTATED FAUNAL LIST

The following contains the standard terminology for cavernicolous animals (see Barr 1968, Peck and Lewis 1978).

PHYLUM ANNELIDA

CLASS OLIGOCHAETA

Family Lumbricidae

Aporrectodea tuberculata (Eisen), D. Schwert det., troglophile-edaphobite.

Little Brush Creek Cave, 3. Big Brush Creek Cave, 5.

Allolobophora sp., D. Schwert det., troglophile-edaphobite.

Big Brush Creek Cave, 1 immature.

Family Enchytraeidae

Genus and species undetermined, troglophile-edaphobite.

Big Brush Creek Cave.

PHYLUM ARTHROPODA

CLASS CRUSTACEA

Order Amphipoda

Family Crangonyctidae

Stygobromus sp., J. Holsinger det., troglobite.

Pole Creek Cave, abundant in flooded passage. These are an undescribed species, very similar to several others in the western *hubbsi* group (Holsinger 1974). This is the first collection of subterranean amphipods from Utah.

CLASS ARACHNIDA

Order Aranea

Family Erigonidae

Anacornia proceps Chamberlin, W.J. Gertsch det., troglophile.

Big Brush Creek, 1 female and 1 immature. Dry Forks Cave, 1 male, 11 females, 8 immatures.

Order Acarina

Family Rhagidiidae

Rhagidia sp., cf. *grahami* Elliott, troglophile or troglobite.

Little Brush Creek Cave (type locality), Sheep Creek Cave, Ice Cave, Big Brush Creek Cave, and Dry Forks Cave. The species was previously reported only from the type locality (Elliott 1976), but the above abundant records may represent other species as well in this poorly known genus.

Family Oribatidae

Genus and species undetermined, troglophile.

Big Brush Creek Cave, abundant on flood debris.

CLASS CHILOPODA

Order Scolopendromorpha

Family Scolopendridae

Genus and species undetermined, accidental?

Big Brush Creek Cave, one in flood debris.

CLASS DIPLOPODA

Order Polydesmoidea

Family, genus, and species undetermined, troglophiles?

Dry Forks Cave. A small eyeless species abundant on damp debris.

CLASS INSECTA

Order Collembola

Family Onychiuridae

Onychiurus decus Christiansen, K. Christiansen det., troglophile.

Big Brush Creek Cave. The species was previously known only from a snowfield in Montana (Christiansen and Bellinger 1980:431).

Onychiurus similis Folsom, K. Christiansen det., troglophile.

Pole Creek Cave. The species is widespread across the United States, with only

one cave record from Texas (Christiansen and Bellinger 1980:437).

Onychiurus ramosus Folsom, K. Christiansen det., troglophile.

Whiterocks Cave, on moist rat dung. The species is widespread across the United States, with only two cave records from Virginia (Christiansen and Bellinger 1980:453).

Family Tomoceridae

Tomocerus flavescens (Tullberg), K. Christiansen det., troglophile.

Big Brush Creek Cave, Little Brush Creek Cave, Pole Creek Cave. Christiansen (1964) notes that the species is spread across the continent and is known from caves in 14 states.

Order Diplura

Family Campodeidae

Haplocampa sp., L. M. Ferguson det., troglobite.

Pole Creek Cave. This is a new species with an unusual morphology. The genus contains cavernicolous species in Illinois, Missouri, California, and Washington; and epigeal species in California, Montana, Oregon, Washington, and Alberta.

Haplocampa sp., L.M. Ferguson det., troglobite.

Sheep Creek Cave, Little Brush Creek Cave, Big Brush Creek Cave. This is a new species and may represent a new genus.

Order Coleoptera

Family Carabidae

Bembidion sp., accidental.

Big Brush Creek Cave, on flood debris.

Rhadine sp., troglophile.

Dry Forks Cave, one dead on sand bank.

Family Staphylinidae

Quedius spelaeus Horn, troglophile.

Dry Forks Cave, many in *Neotoma* dung and nest debris. The species occurs across the continent, frequently in caves (Smetana 1971).

Genus and species undetermined, troglophile?

Ice Cave, two in entrance debris. These are in the subfamily Aleocharinae, which is frequently found in caves.

Family Scarabaeidae

Aphodius sp., accidental.

Ice Cave, three in entrance debris.

Order Lepidoptera

Family Noctuidae

Euxoa auxiliaris (Grote), D. LaFontaine det., troglaxene.

Ice Cave. This and the following species of fairly widespread moths often retreat to caves to aestivate or to seek a daytime retreat.

Euxoa idahoensis (Grote), D. LaFontaine det., troglaxene.

Ice Cave.

Apamea amputatrix (Fitch), D. LaFontaine det., troglaxene.

Ice Cave.

Scoliopteryx libatrix (Linnaeus), troglaxene.

Pole Creek Cave. The species is worldwide, and commonly uses caves as overwintering sites.

Order Siphonaptera

Family Ceratophyllidae

Orchopeas sexdentatus (Baker), G. Holland det., ectoparasite.

This is a widespread flea on *Neotoma* wood rats, and these specimens were abundant in a *Neotoma* nest in Dry Forks Cave.

Order Diptera

Family Tipulidae

Pterelachisus sp., H. Teskey det., troglaxene.

Ice Cave, on ceiling.

Yamatipula sp., H. Teskey det., troglaxene.

Ice Cave, on ceiling.

Family Mycetophilidae

Rymosia sp., R. Vockeroth det., troglaxene.

White Rocks Cave, Ice Cave.

Bolitophila sp., R. Vockeroth det., troglaxene.

Ice Cave.

Bolitina sp., R. Vockeroth det., troglaxene.

Ice Cave.

Exechia sp., R. Vockeroth, troglaxene.

Ice Cave.

Exechiopsis sp., R. Vockeroth det., troglaxene.

Pole Creek Cave, abundant 'on ceiling at entrance; Ice Cave.

Mycetophila sp., R. Vockeroth det., troglaxene.

Ice Cave.

Family Sciaridae

Lycoriella sp., R. Vockeroth det., troglaxene or troglophile.

White Rocks Cave, Dry Forks Cave.

Family Spherozeridae

Leptocera sp., R. Vockeroth det., troglone or troglophile.

Ice Cave, Dry Forks Cave.

Family Phoridae

Megascelia sp., R. Vockeroth det., troglone or troglophile.

Ice Cave.

Family Heleomyzidae

Genus and species undetermined, troglone or troglophile.

Ice Cave.

Family Anthomyidae

Genus and species undetermined, accidental.

Ice Cave.

DISCUSSION

A total of 38 species were found in caves in the Uinta Mountains. Of these, 30 species are in taxa that are typical of caves and cave-like habitats in North America in their behavioral, ecological, and evolutionary characteristics. The only true cave-limited species are the amphipod, 2 dipturans, and possibly the *Rhadidia* mite.

As habitats, the caves themselves are probably preglacial in time of origin, especially White Rocks Cave. The caves may not have been overridden by the Pleistocene piedmont and valley glaciers coming from the Uinta Mountain uplands (Atwood 1904, Hansen 1975), but they would have suffered extreme and prolonged flooding and scouring by meltwater streams. The caves were probably uninhabited during glacials because they were colder, there was less food input due to periglacial climatic conditions, and because of meltwater scouring. Thus, the fauna probably represents an occupation of caves sometime in the past 10,000 years since the last glacial. In this respect the fauna is very similar to that of Ontario, Canada, caves which have been occupied since the last glacial, and have an abundance of troglone diptera (Peck, unpubl. ms.).

The amphipod may be an exception to this generalization. Holsinger (1980) thinks that some groundwater amphipods may have existed under glacial ice masses, but I am inclined to keep open the alternative of movement from unglaciated peripheral refugia, through interstices in groundwater, into the

area after deglaciation (Peck and Lewis 1978). A large fauna is known to live in the west in the interstices of gravels and coarse streamside sediments (Stanford and Gaufin 1974), which knowledge supports the possibility of such faunal movements.

Future research can contribute by surveying cave faunas in the western Uintas. The area of greatest present ignorance of cave faunas is in the details of their life cycles and seasonal dynamics. Most rewarding would be careful ecological study of the troglobites or of the troglone diptera.

ACKNOWLEDGMENTS

We thank Forest Ranger Mike Bergfeld and Forest Recreation Officer Tom Contreras of the Vernal U.S. Forest Service Office for allowing study in White Rocks Cave. The field work was supported by operating grants of the Canadian Natural Sciences and Engineering Research Council to investigate the distribution and ecology of subterranean faunas. The help of the many taxonomists with determinations is deeply appreciated.

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EVALUATING THE RELATIONSHIP BETWEEN MULE DEER PELLET-GROUP DATA AND AVAILABLE WINTER RANGE, USING LANDSAT IMAGERY

John W. Wyckoff

ABSTRACT.— In this study, mule deer population trend data (deer-days-use/hectare) were statistically analyzed with range area data that were extracted from LANDSAT satellite imagery. The remote sensing techniques developed use multitemporal, winter images of an area in central Utah. Snow-covered areas and vegetational areas mapped from the imagery were composited into 26 maps representing the approximate winter range available to mule deer on 26 dates over a five-year period (1972–1977). Utah State Division of Wildlife Resources pellet-group transect data were statistically analyzed with range data measured from the satellite imagery. Range area accounted for a fairly large proportion of the variation in deer-days-use/hectare ($r = -.83$). This result seems reasonable since deer population density should increase as available range decreases.

In this study the relationship between vegetational area defined by the extent of snow cover and mule deer pellet-group transect data are examined. LANDSAT satellite imagery was used as a means of measuring the distribution of snow cover and vegetation in an area of central Utah between 1972 and 1977.

Researchers studying deer population dynamics agree that snow cover and winter range are critical limiting factors of deer populations (Aldous 1945, Anderson et al. 1974, Dasmann and Hjersman 1958, Gilbert et al. 1970, Leopold et al. 1951, Levaas 1958, Richens 1967, Wallmo et al. 1977). Use of remote sensing techniques for analyzing wildlife populations and wildlife habitat is not a recent development. Low altitude aerial photograph interpretation has been a commonly employed technique since the mid-1930s for vegetational analysis (Dalke 1937, 1941, Leedy 1948) and for direct censusing of wildlife populations (Heyland 1975, Meier 1975).

In the past 20 years, development of new sensing systems has generated an intense interest among wildlife biologists in the application of new remote sensing techniques. Many standard field procedures used to study wildlife are laborious and time consuming, and the prospect of gaining data more rapidly has prompted much of the current interest in remote sensing. Among the more recently developed sensors that augment conventional aerial photography in wildlife investigations

are radar, thermal infrared scanners, and multispectral scanners. Platforms that contain these sensor packages are midaltitude commercial aircraft, high altitude U-2 and RB-57, and NASA's LANDSAT satellites. NASA's LANDSAT program began in the summer of 1972 with the launching of LANDSAT 1 (formerly called ERTS 1) and has continued with the launching of two subsequent satellites (LANDSAT 2 and 3) (U.S. Geological Survey 1979). Because these satellites retrieve data from the same geographic area every 18 days, this new technology provides wildlife managers with the potential of repeated monitoring of wildlife habitat.

In addition to wildlife and vegetation studies, the LANDSAT satellites are a useful data source for numerous other resource studies. One approach important to the present research was initially developed to monitor the variable of winter snow cover in montane hydrologic cycles (Aul and Ffolliott 1975, Barnes 1974, Evans 1974, Meier 1975, Rango 1975). In these LANDSAT snow surveys, visual interpretation of enlarged imagery (scale = 1:250,000) was an accurate means of mapping the areal extent of snow cover. Snow cover and winter range are agreed to be important to deer population dynamics, and it has been demonstrated that LANDSAT is capable of detecting changes in snow cover. With these two factors taken into consideration, this project was undertaken to refine

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a remote sensing technique that would utilize snow measurements made from satellite imagery for predicting regional deer population trends.

STUDY AREA

The study area (Fig. 1), which lies mainly along the Wasatch Plateau in central Utah, is

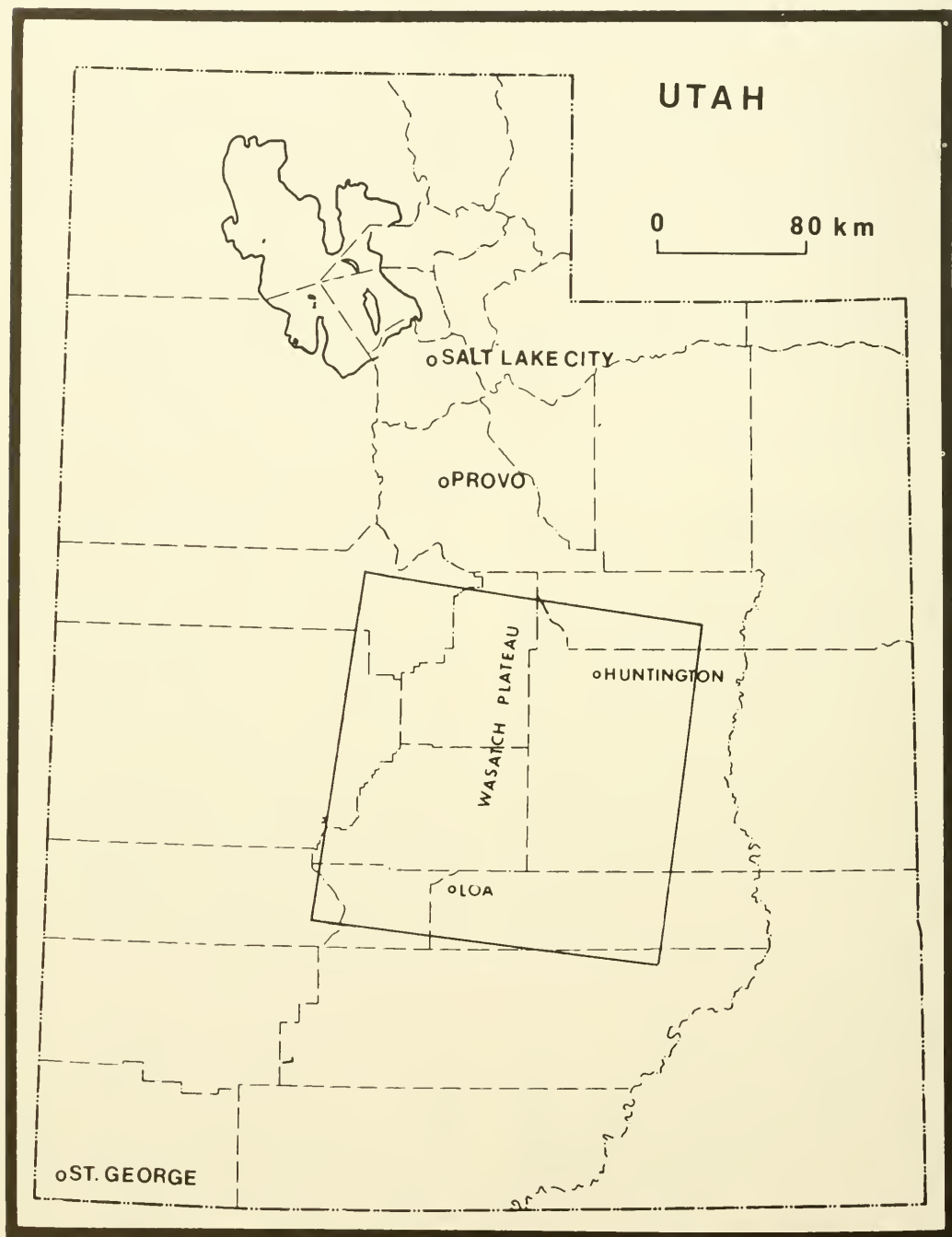


Fig. 1. Location of the study area within Utah. Boundaries are not aligned directly north and south because of the orbital paths of the LANDSAT satellites.

physically complex and consists of dominant, north-south-oriented mountain ranges dissected by low valleys. Physiographic features included in the study area include the Wasatch Plateau, the Sevier Plateau, and the southern tip of the Wasatch Mountains. Vegetation of this area reflects both the complexity of the physical environmental patterns and their apparent modifications by man. Areas modified by man support a combination of agricultural land uses including dry farming (nonirrigated) of winter wheat, irrigated farming of alfalfa, and pasturage of livestock (mainly sheep and cattle). Less disturbed areas of the valleys are dominated by desert shrub species relatively common throughout the cold desert. They include big sage (*Artemisia tridentata*), rabbit brush (*Chrysothamnus nauseosus*), Mormon tea (*Ephedra viridis*), bromegrass (*Bromus* spp.), wheatgrass (*Agropyron* spp.), and grama (*Bouteloua* spp.). Along a hypothetical transect from the low valleys to the mountain crest, the undisturbed vegetation communities above the valley floors form four plant zones that vary according to environmental gradients of temperature and moisture. The first communities to be encountered above the previously described desert shrub communities are either deciduous shrub (*Acer grandidentatum*-*Quercus gambelii*) or juniper-pinyon (*Juniperus* spp.-*Pinus edulis*). These two communities occur in approximately the same elevational range and are segregated primarily by differences in available moisture, with deciduous shrub communities occurring in the more mesic sites. The second elevational zone comprises a combination of forested plant communities, but the dominant community in the study area is aspen (*Populus tremuloides*). Scattered among this dominant community are relatively homogenous stands of the Douglas fir-white fir community type (*Pseudotsuga menziesii*-*Abies concolor*); these localized stands are also apparently controlled by local site factors. At higher elevations the communities in the third elevational zone make a gradual transition to spruce-fir (*Picea engelmannii*-*Abies lasiocarpa*). The uppermost community or fourth elevational zone encountered in this transect is alpine tundra (various mat-forming species), which reflects the combination

of dessication (frost and wind) and poor soil formation at the highest elevations of this area (Allred 1975, Arnow and Wyckoff 1977, Buchanan and Nebeker 1971). Within the study area (Fig. 1) are 15 deer herd management units, whose boundaries are defined by the Utah State Division of Wildlife Resources (DWR). These herd units (Fig. 2) are the basis for the state's retrieval of deer population data and the implementation of deer management regulations. They are also the areas from which deer population data are analyzed in this study.

METHODS

Data for this study were extracted from two primary sources. The first source was a report published by the Utah State Division of Wildlife Resources (1978) that provided detailed data from pellet-group transects within the study area. The second major data source for this study consisted of imagery from the NASA LANDSAT satellites. Satellite imagery was used for mapping of vegetation distribution and seasonal distribution of snow cover. Vegetation interpretation and mapping was carried out on a false-color composite LANDSAT image at a scale of 1:250,000, dated 25 August 1977 and processed to a positive print. Because of the small scale of the image, detailed vegetation interpretation was not carried out. Instead, the vegetational boundaries mapped consisted of the interface between oak-maple or pinyon-juniper communities and desert shrub communities. This boundary is significant because it approximates the lower elevational limits of vegetation types considered suitable for deer wintering (Leopold 1951, Richens 1967). So, per se, the map discussed was not a map of vegetational species, but rather a map showing the lower elevational extent of all vegetation types considered by many as suitable winter range for mule deer. As this vegetational boundary was interpreted on the image it was traced directly onto an acetate (stable drafting film) overlay. After this map was completed it was photographically reduced to a scale of 1:500,000 (50 percent reduction) and processed to a film positive print. Snow cover was mapped using 70 mm black and white LANDSAT band 5 transparencies (1:3,000,000) and a color additive

viewer that enlarged the 70 mm transparencies to a mappable scale (1:500,000). Mapping of snow cover consisted of delineating a boundary along which snow was present on one side and absent on the other. No attempt was made in this study to differentiate snow depths from satellite imagery. Although it is well known that snow depth and snow condition (ice crusts, etc.) both have a strong influence on deer distribution (Gilbert

et al. 1970) these parameters were not detectable on the LANDSAT imagery used in this research. The rationale for using simply presence or absence as a measure was that, as snow accumulates and extends to lower elevations or ablates and recedes to higher elevations, the areal extent of snow in itself should represent a general shrinking or enlarging of available winter areas for deer. After the individual images were enlarged into

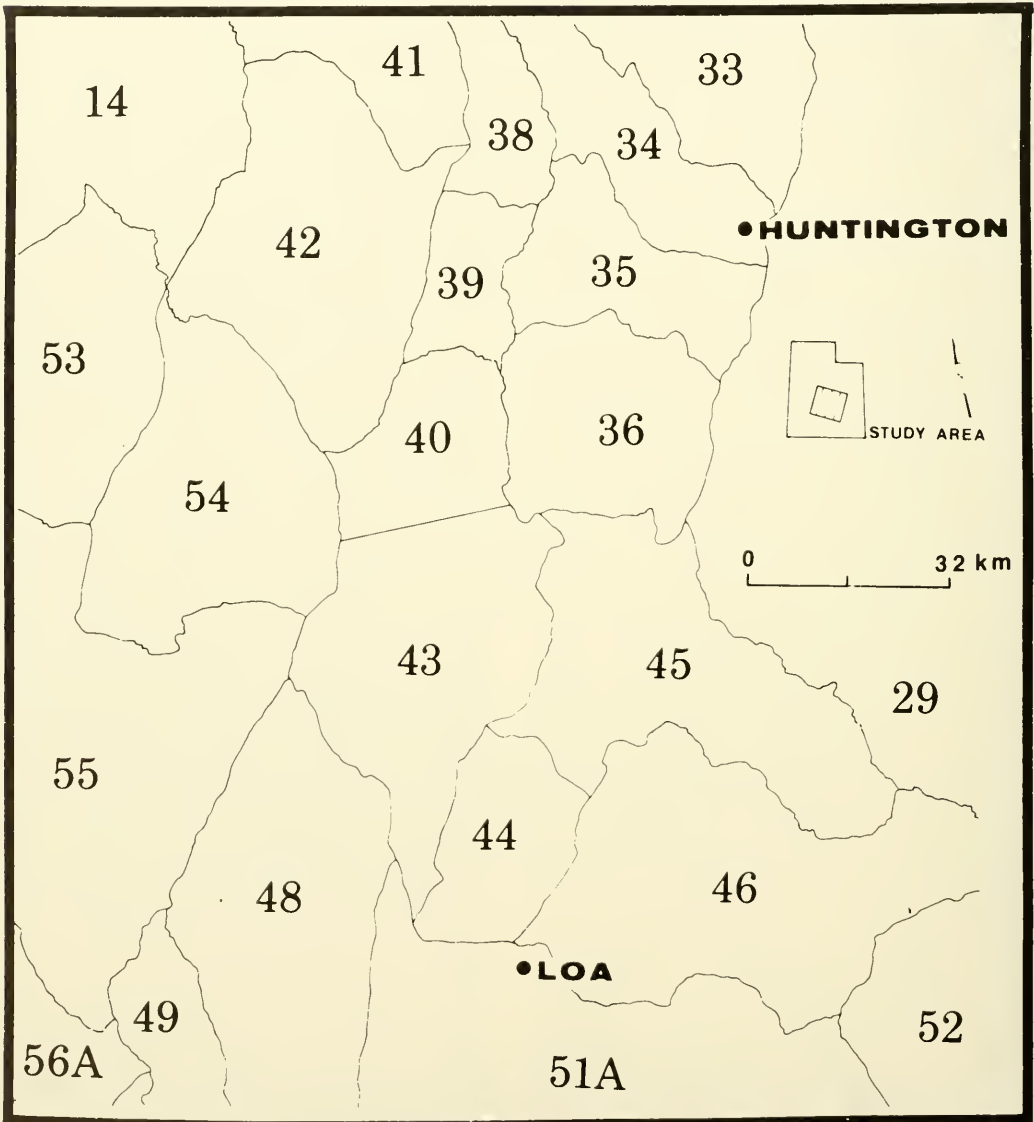


Fig. 2. Locations of the Utah State Division of Wildlife Resources deer herd management units in the study area.

the drafting surface of the color additive viewer, the snow boundary was traced manually onto an acetate overlay. Snow cover was mapped for a period extending from the winter of 1972-73 to the winter of 1976-77. In all, 30 LANDSAT images of different dates were interpreted and mapped for snow cover (Table 1). Although the satellites each cover the same ground scene every 18 days, cloud cover during the winter period limited the acquisition of 18-day repetitive coverage of the study area.

In the last phase of the mapping procedure, the snow cover maps were composited with the vegetation map to form the final maps, which portray the distribution of vegetation assumed to be suitable for deer winter range at given points in time. After the composite maps were produced, the winter range areas were measured with a Hewlett-Packard Model 9866A microcomputer that was interfaced with a map board and cursor. The microcomputer was programmed as an electronic planimeter to automatically

compute area from the map scale. As a result of the composite mapping, 26 maps (four images indicated total snow cover and were therefore not mapped) were produced, which illustrate the annual variation, in the mapped winter range, over a five-year period (Fig. 3). Data from both sources were compiled into two separate sets of observations. This compilation was accomplished by dividing the study area into two distinct geographic units (Fig. 4). DWR pellet-group transect data were placed in the observations of the first or second geographic unit and analyzed with vegetational area data from that same area. This summarization of herd unit data from the 15 DWR-designated units was carried out because of a lack of any real barriers to deer migration between most of the DWR units. The boundary that separated the herd units into two distinct geographic units was placed along the center of a broad, low-elevation valley with heavy agricultural use. Because of sparse vegetation this may be a more realistic barrier to deer migration and, therefore, a reasonable separation of populations. After compiling the data in this fashion (Table 2), the vegetational data extracted from satellite imagery and the DWR transect data were analyzed by regression (Nie et al. 1975).

TABLE 1. Dates of LANDSAT satellite imagery acquired for analysis of snow cover and vegetation.

2 February 1973
15 April 1973
3 May 1973
8 June 1973
30 October 1973
15 February 1974
28 April 1974
16 May 1974
26 June 1974
19 September 1974
25 October 1974
30 November 1974
5 January 1975
28 February 1975
5 April 1975
11 May 1975
25 June 1975
20 October 1975
4 December 1975
18 January 1976
27 January 1976
21 March 1976
30 March 1976
14 May 1976
26 June 1976
5 October 1976
14 October 1976
28 November 1976
16 December 1976
9 April 1977

RESULTS AND DISCUSSION

Regression analysis of the data (Fig. 5) supports the assumption of a relationship between range area measured with the remote

TABLE 2. Data for deer population with observations based on areas corresponding to Figure 4.

Area	Year	Mean deer-days-use/ hectare	Mean square kilometers of winter range
1	1973	61.0	1538.5
	1974	56.2	1834.2
	1975	69.3	2110.3
	1976	40.1	2892.5
	1977	29.7	4133.9
2	1973	128.0	1154.1
	1974	99.0	1533.0
	1975	94.1	1427.6
	1976	72.5	1915.0
	1977	44.6	3014.0

Area 1 corresponds to DWR herd units 34, 35, 36, 45, 46, 51A, 38, 39, 40, 43, and 44.

Area 2 corresponds to DWR herd units 42, 54, 48, 53, and 59.

sensing technique and the DWR pellet-group transect measure of deer-days-use/hectare ($r = -.83$, $P < .003$). These results seem logical, even though in this research there was no direct consideration of the important snow parameters mentioned earlier (i.e., snow depth and snow condition), since it would be ex-

pected that seasonal shifts in snow elevation through accumulation and ablation would, perhaps, influence these parameters. The negative relationship demonstrated by these analyses would seem reasonable because, as snow cover increased over the suitable vegetation types, causing a shrinkage of winter

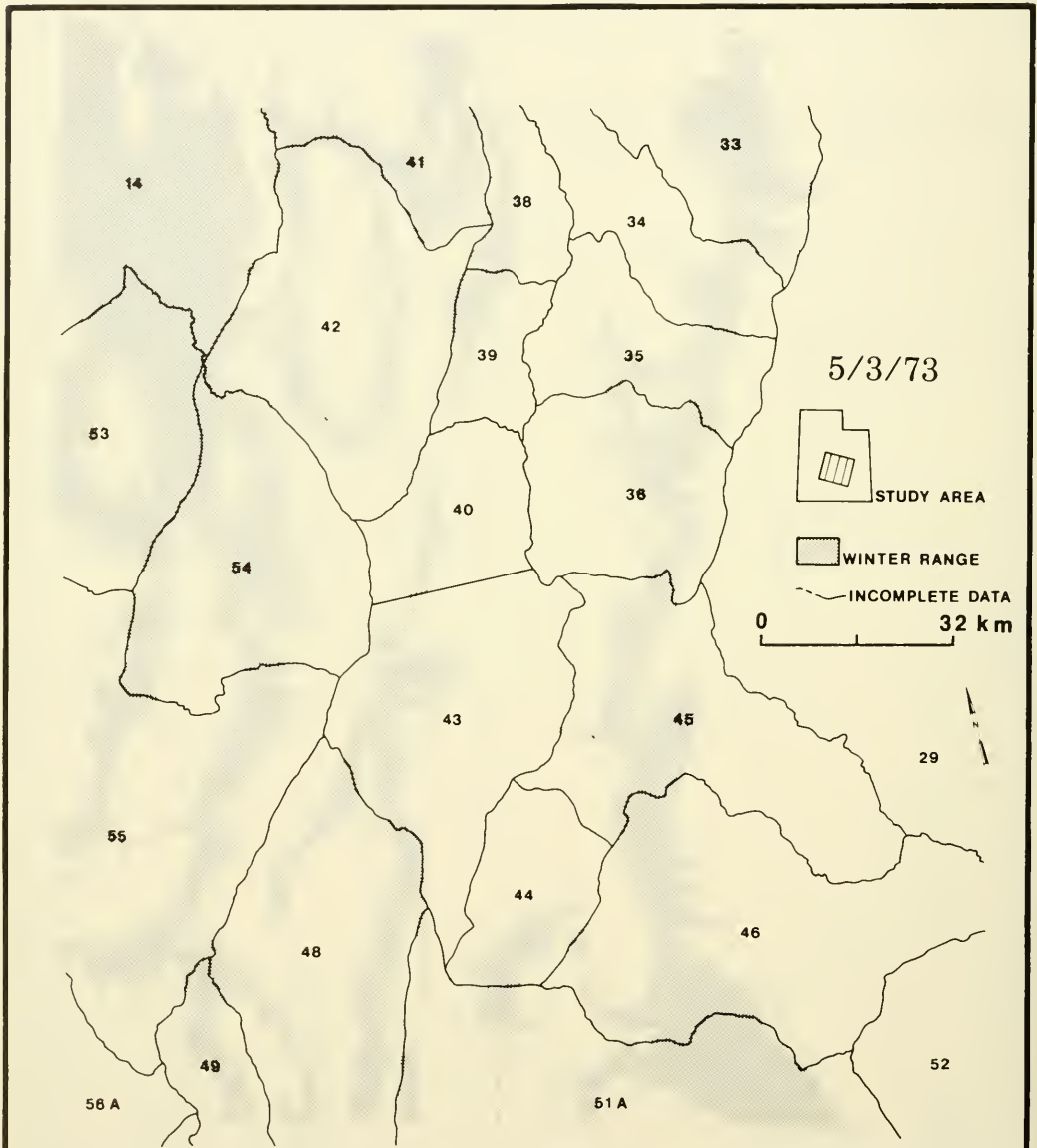


Fig. 3. Sample composite map (1 of 26) that is the result of combining a snow cover map (generated from the interpretation of satellite imagery), a map of the lower boundary of deer habitat (interpreted from satellite imagery), and a map of the state defined herd unit boundaries (delimited by legal description onto a 1:250,000 U.S.G.S. quadrangle). Each of the maps that were developed represent deer winter range available on the date the satellite imagery was acquired.

range, deer use would tend to increase per unit area of available range. This finding may have several important management implications: as a new technique for assessing winter ranges over large areas in a relatively short time, for evaluating land areas for acquisition by the state for winter range preservation, and for analyzing the effects of winter cloud seeding on deer ranges.

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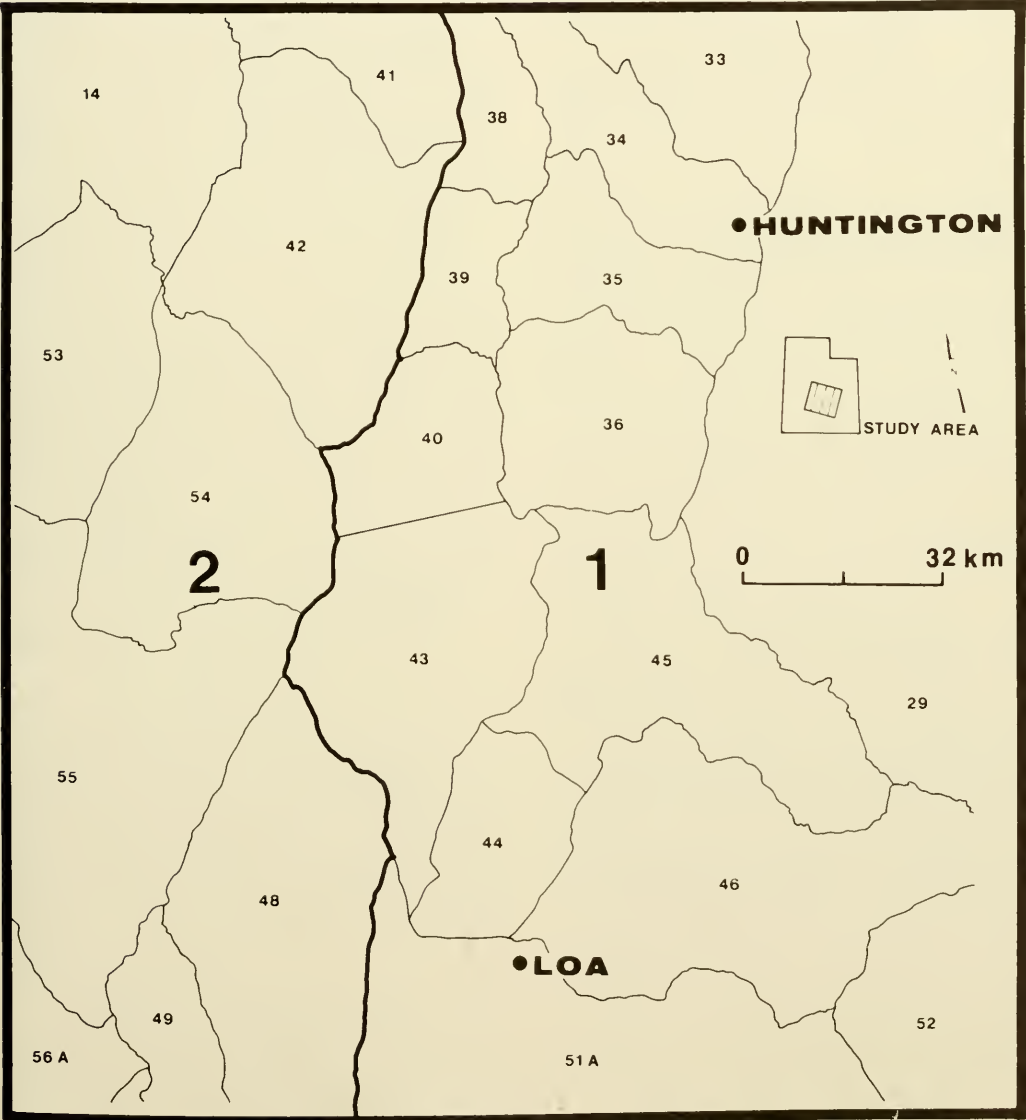


Fig. 4. Study area showing the boundary that was used to divide the herd units into more biologically appropriate samples.

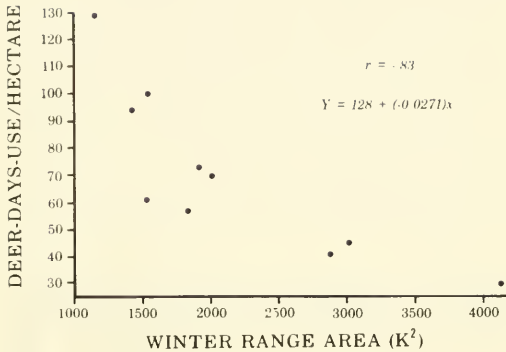


Fig. 5. Regression of the variable deer-days-use/hectare with winter range area using the data compiled within the two more biologically appropriate subsamples ($n = 10$).

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TIME BUDGETS OF WYOMING GROUND SQUIRRELS, *SPERMOPHILUS ELEGANS*

David A. Zegers¹

ABSTRACT.— Time budget of free-living adult *Spermophilus elegans* differed significantly from that of juveniles in the Front Range of the Rockies during 1974–1975. No differences were found between males and females. Hour of day, day since emergence, air temperature, cloud cover, and presence of predators all correlated with the frequency of various components of the time budget.

Study of time budgets is important in comprehending the roles of animals in ecosystems as well as understanding their basic patterns of behavior. Time budgets constructed for a few ground squirrels [the Columbian ground squirrel, *Spermophilus columbianus* (Betts 1976); the thirteen-lined ground squirrel, *S. tridecemlineatus*, and the spotted ground squirrel, *S. spilosoma* (Streubel 1975); and Belding ground squirrel, *S. belding* (Morton 1975)] illustrate the significant effects exogenous and endogenous factors have on the time allotted to various activities. My objectives were (1) to produce time budgets for the Wyoming ground squirrel, *Spermophilus elegans* (*sensu* Nadler, Hoffmann, and Greer 1971; (2) to document differences in time budgets due to age and sex; (3) to correlate variation in time budget with several environmental factors: weather, day since emergence, hour of day, and presence of predators; and (4) to assess the ecological and evolutionary correlates of these variations in time budget.

METHODS

A colony of free-ranging Wyoming ground squirrels was observed from 18 May 1974 to 24 August 1974 and from 20 April 1975 to 20 August 1975 in a montane meadow (2440 m elevation) in the Front Range of the Rocky Mountains approximately 16 km southwest of Boulder, Colorado (Zegers and Williams 1979).

Using the technique of Wiens et al. (1970), I employed an electronic metronome,

binocular, and a 20X telescope to observe the squirrels from a blind. The animals were marked for individual recognition from a distance using a unique combination of freeze brands (Hadow 1972) located at one or two of the spots on the animal's body.

The behavior of these ground squirrels was divided into 13 categories (i.e., activities) (Zegers 1977). This classification scheme is similar to those previously used for this squirrel (Clark and Denniston 1970) and for the closely related Richardson's ground squirrel, *S. richardsonii* (Quanstrom 1968 and 1971). These 13 activities and their definitions are as follows:

1. The basic posture is a resting and observation position with all four paws on the ground.
2. Semi-alert posture is a resting and observation position in which the forepaws are off the ground and the back is arched.
3. The alert position is a resting and observation position in which the forepaws are off the ground and the back is straight, not arched.
4. The down feeding posture is a variation of the basic posture in which the squirrel is eating. Food is manipulated using the teeth and lips without the aid of the forepaws.
5. The upright feeding posture is a variation of either the semi-alert or alert postures in which food is handled with the forepaws.
6. Running is a rapid locomotor activity in which the animal is moving ≥ 1.0 m/s and is not involved in a chase.
7. Chasing is running in which the individual is chasing another.
8. Chased is running in which the individual is being chased.
9. Walking is relatively slow (compared to running) locomotion of < 1.0 m/s.
10. Hay-gathering involves stuffing herbaceous stems and leaves into the mouth without chewing and

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swallowing. These materials are cut or pulled up by use of the forepaws and teeth and placed in the mouth perpendicular to the sagittal line and then deposited somewhere underground.

11. Grooming includes self- and allogrooming as well as dusting, in which a squirrel rolls from side to side while prostrate in the dirt of an entrance mound.
12. Digging is the behavior in which a squirrel removes soil from a tunnel entrance by using either or both hind limbs and forelimbs.
13. Fighting is similar to fighting among other rodents, and involves rolling, biting, clawing, and yelping.

Other data were collected for each of 1125 observation periods, which lasted from 5 to 15 minutes. These data included date, time of observations, animal identification number, information about predators (i.e., whether or not a predator was visible, and, if so, its species), and weather conditions. Air temperature was measured at 0.5 m above ground every half hour. Sky cover was divided into four cloud categories: clear (no clouds), partly cloudy (less than 50 percent of sky covered), mostly cloudy (more than 50 percent of sky covered) and overcast (complete cloud cover).

Differences in time budget due to age and sex were tested via chi-square analysis. The relationship between five environmental factors and the components of time budget were analyzed by multiple regression. Air temperature, day since emergence, hours of day, sky conditions, and presence of predators served as independent variables, and the frequencies of each of the 13 activities for each of the observation periods were the dependent variables.

RESULTS AND DISCUSSION

Although the behavior of *S. elegans* has been studied (Clark 1970a, Clark and Denniston 1970, Pfeifer 1980), a time budget has never before been constructed. Aboveground time budget for all individuals is shown in Figure 1. Note that the two feeding activities were the most protracted, combining to consume 39.3 percent of all time spent above ground. The three sedentary but watchful positions (basic, semi-alert, and alert) were the next most frequent, followed by the five postures labeled "individual maintenance." Note that the three agonistic activities were the least frequent.

Few time budgets of other sciurids are available for comparison. Betts (1976) found that feeding consumed from 49 to 86 percent, and "alertness" occupied from 6 to 26 percent of the total time above ground of *Spermophilus columbianus*. *Tamiasciurus*, the red squirrel, spent approximately 35 percent of its total time above ground feeding, although this percentage ranged from 9 to 60 percent (Smith 1968). Streubel (1975) found *Spermophilus tridecemlineatus* spent 42.4 percent and *S. spilosoma* spent 45.6 percent of its time feeding, but only 11.6 percent and 15 percent, respectively, in some alert postures. Sexual and agonistic behavior comprised less than 5 percent of the total budget for these species. When above ground, Wyoming ground squirrels spent a smaller proportion of their time feeding, and more time in sedentary observation than these other species. This may be due to a greater threat from predators, or to prevailing habitat conditions resulting in differences in social system or foraging strategy.

These differences in time budget also reflect differences in territorial maintenance strategy. For example, *Tamiasciurus*, a squirrel that defends a food supply, uses a strategy that spends little time on actual territorial defense (0.25 to 1.85 percent of active time, Smith 1968). Complete defense is probably difficult if not impossible in the spatial complexity of the coniferous forest. It appears to be energetically adaptive to use warning calls and to tolerate some intrusion rather than to spend considerable time and energy chasing other squirrels. *Spermophilus spilosoma* and *S. tridecemlineatus* do not defend food supplies. Their territoriality can be described as core monopolization (Streubel 1975), in which individual distance and the tendency to remain near the home burrow spaces individuals. No cooperative or extended familiar behavior and little agonistic behavior occur (Streubel 1975). In contrast, *S. richardsonii* and *S. elegans* do not defend food territories but do defend reproductive territories. During mating individual males occupy territories that contain the home ranges of several females (Yeaton 1972). These are succeeded by female territories during gestation and lactation (Quanstrom 1968, Yeaton 1972). My observation of female territories for *S.*

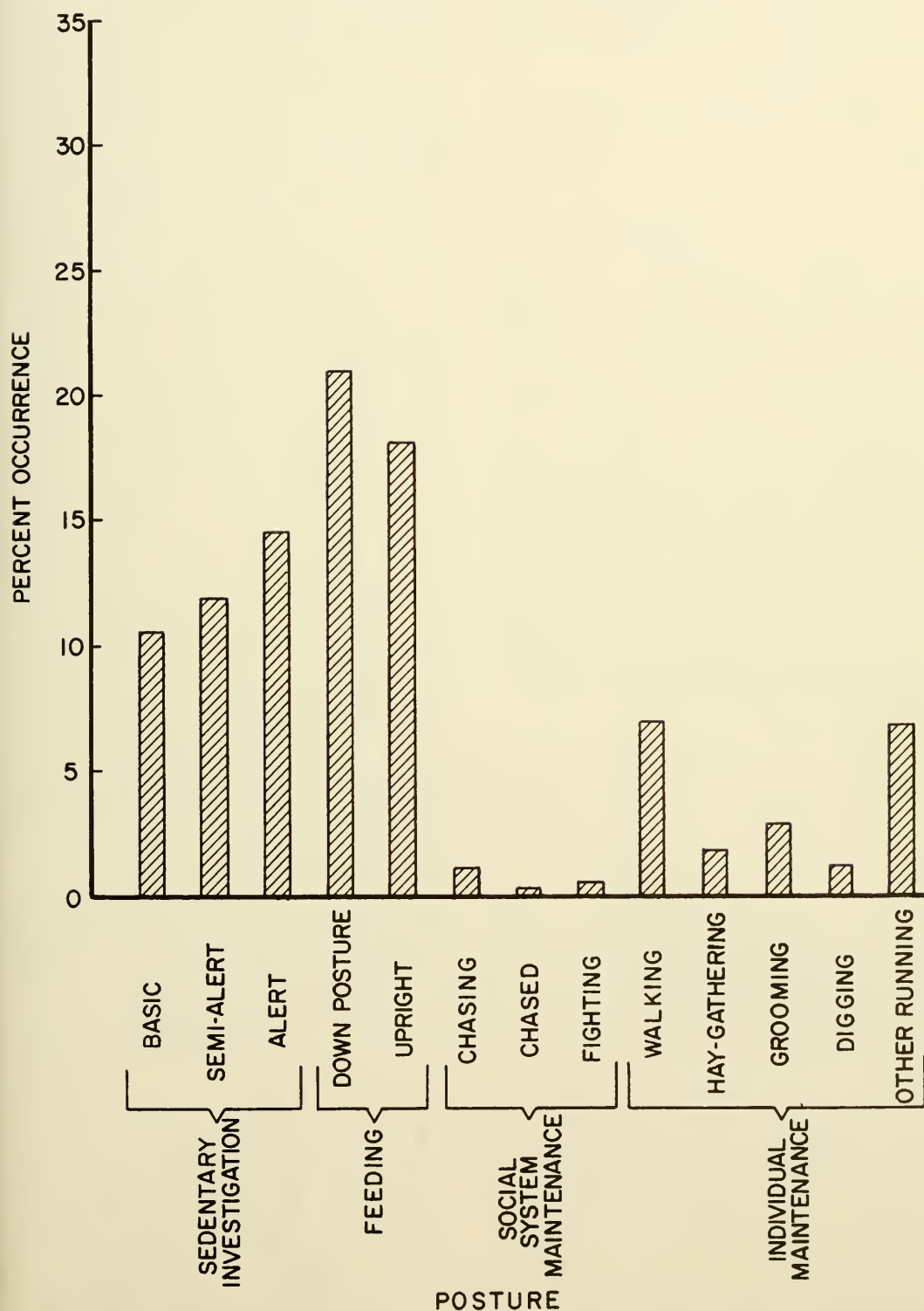


Fig. 1. Time budget of a population of Wyoming ground squirrels during the summers of 1974 and 1975.

elegans revealed them to be essentially used to protect the burrow entrance, (and therefore the young) against intrusion by conspecifics rather than for defending an area of open ground.

The differences in time budget between sexes for adults and between age groups are shown in Figures 2 and 3. Time budgets of adults differed significantly from those of juveniles ($X^2 = 38.67$; $df = 12$; $p < 0.05$) but sex did not have a significant effect on time budget ($X^2 = 0.73$; $df = 12$; $p > 0.05$). The effects of age and sex on time budgets have not been studied extensively for sciurids. I know of only one other study of sciurids that presents time budget data by age and sex groups. Although the data were not statistically analyzed, the time budgets of adult and yearling *S. columbianus* appear to be substantially different from those of juveniles (Betts 1976). Moreover, differences between adults and yearlings and between males and females existed. Likewise, my data indicate a significant difference between age groups, although the difference between sexes was not significant. The apparent time budget differences between sexes of the Columbian ground squirrel suggest that that species has a more pronounced division of labor than *S. elegans*.

Differences in time budget between adults and juveniles are important and obvious. Feeding to support growth is not as important to adults as to juveniles. Adults come out

of hibernation essentially full grown and must only consume sufficient energy to reproduce successfully and to deposit enough fat to survive hibernation. Juveniles, however, grow at a rate of 11.4 percent per day during the first weeks after birth until full length is achieved at about 63 days of age (Clark 1970a). In addition, the juveniles must then put on enough fat to survive hibernation. Moreover, for both *S. richardsonii* and *S. elegans* a temporal difference exists between adults and juveniles in their activities. Adults are finished with aboveground activities before juveniles start prehibernatory fattening (Clark 1970b, Dorrance 1974, Michener 1972 and 1974, Quanstrom 1968, and Zegers 1977). This removes adults from the area when the juveniles are preparing for hibernation and, by reducing intraspecific competition, probably increases survival of juveniles (Yeaton 1969). Likewise, early immergence of adults into hibernacula may increase adult survivorship by reducing predation pressure (Morton 1975).

Several sciurids are known to modify activity periods in response to environmental factors (Yeaton 1969, Clark 1970b, Quanstrom 1971, Baudinette 1972, G. R. Michener 1973). Multiple regression of environmental factors on the 13 components of the time budget of Wyoming ground squirrels revealed some interesting relationships to that budget (Table 1). None of the independent variables correlated with frequency of

TABLE 1. Independent variables which were significant predictors of the frequency of 13 activities of *Spermophilus elegans*. Presence of predator (Pred), hour of day, day since emergence, air temperature, and sky conditions were analyzed for their effect on the frequency of each activity. Direction of the correlation is indicated by the sign (+ or -). n.s. = not significant

Activity	Independent variables ($p < 0.05$ for beta)				
	Pred	Hour	Day	Temp	Cloudiness
Basic	n.s.	+	n.s.	-	n.s.
Semi-alert	+	n.s.	-	-	n.s.
Alert	+	n.s.	n.s.	+	n.s.
Feeding down	-	+	n.s.	-	n.s.
Feeding upright	-	-	+	+	n.s.
Chasing	-	n.s.	+	n.s.	n.s.
Chased	-	n.s.	+	n.s.	-
Other running	-	n.s.	-	n.s.	+
Walking	-	-	-	-	n.s.
Hay gathering	-	-	n.s.	n.s.	n.s.
Grooming	-	n.s.	+	n.s.	n.s.
Digging	-	+	n.s.	-	-
Fighting	n.s.	n.s.	n.s.	n.s.	n.s.

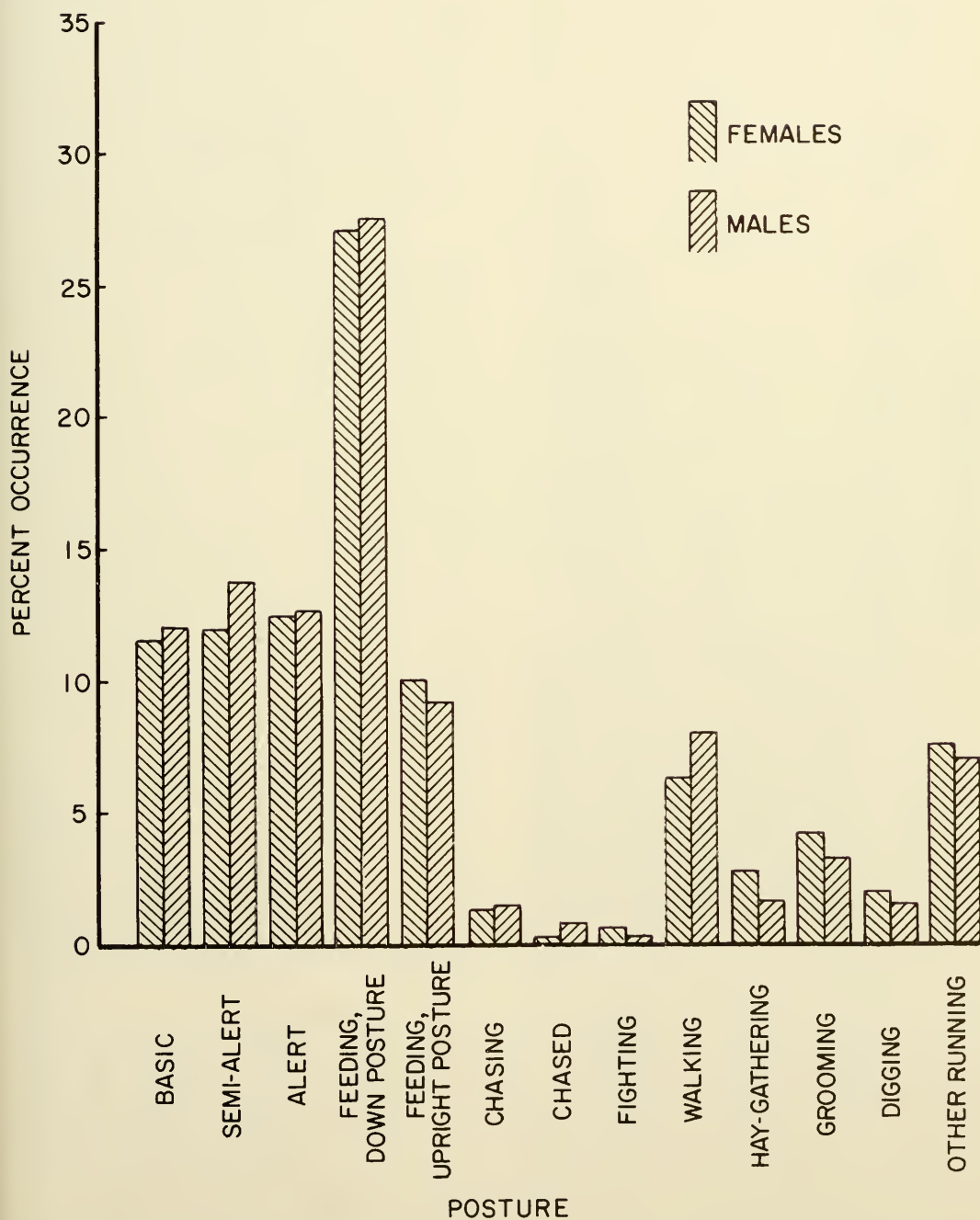


Fig. 2. Comparison of time budgets of adult male and adult female Wyoming ground squirrels during the summers of 1974 and 1975.

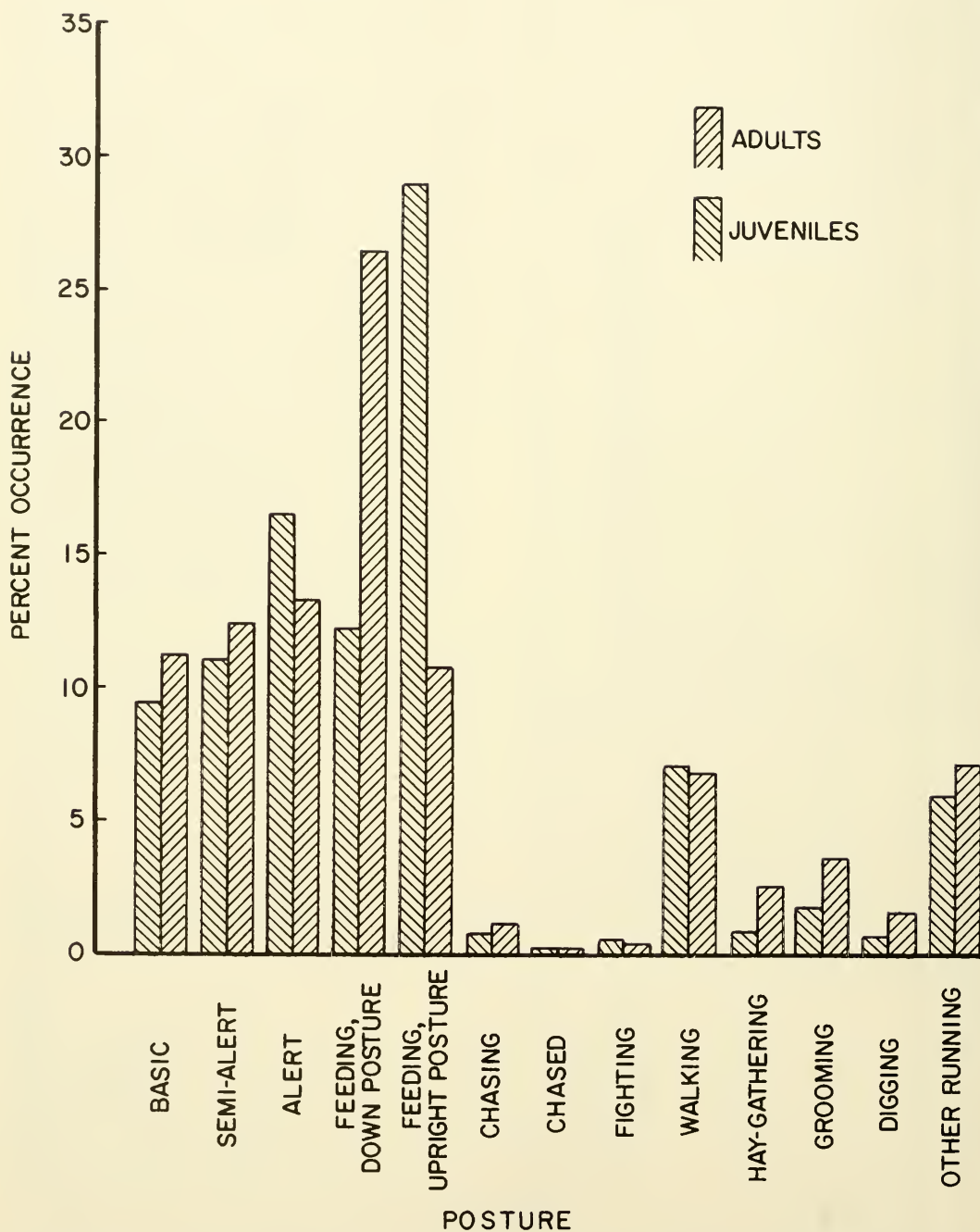


Fig. 3. Comparison of time budgets of all adult and juvenile Wyoming ground squirrels during the summers of 1974 and 1975.

fighting. This reflects the obvious social nature of fighting; social situation was obviously the most important factor in initiating fighting, which went on regardless of the hour, date, or weather.

The presence of a predator was the most recurring significant variable (Table 1), correlating with the frequency of 11 activities. The most casual observer of these squirrels would agree that behavior is greatly modified once a predator is detected by the squirrels. All feeding, social activity, grooming, etc., stopped as the squirrels, using either the basic, semi-alert, or alert postures, intently observed the predator.

Day since emergence correlated with feeding postures, chasing, chased, walking, and grooming activities. This indicates chronological changes in the time budget (Zegers 1977). As the season proceeded, adults became progressively more sedentary and spent less time feeding, although they continued to gain weight (Zegers and Williams 1977). This quiescence could be due to diminished metabolic rate during prehibernatory fattening (Armitage and Schulenberger 1972). In addition, the squirrels might have been able to spend less time feeding and still gain weight because the energy drain of reproduction and territorial defense was no longer present. Regardless of the cause of their quiescence, the alertness of these individuals probably aided in predator detection and thereby contributed to the survival of juveniles. This interpretation is supported by the fact that in the last two weeks before disappearing into hibernacula these adults stopped gaining weight and on the average actually lost weight (Zegers and Williams 1977). Some factor other than insufficient body fat was preventing these adults from hibernating two weeks earlier. Perhaps this factor was parental care.

The effects of ambient temperature, cloud cover, and hour of the day on sciurid time budgets are generally interpreted as thermoregulatory and water balance mechanisms. Michener (1968) demonstrated that *S. richardsonii* modified overall activity in response to air temperature and light intensity (i.e., cloudiness) in ways that promoted overall maintenance of body temperature and water balance. My data show that air temperature

and cloudiness also affect specific behaviors, although this conclusion must be qualified. Many behaviors were not influenced by weather conditions (Table 1). Although running decreased on sunny days, digging increased. As air temperature increased squirrels walked and dug less. This may reflect generally lower activity when temperatures are high. Although this could be a thermoregulatory response, the data in Table 1 generally support the idea that specific behaviors of ground squirrels tend not to be greatly influenced by weather conditions. These squirrels were above ground apparently for a purpose (e.g., feeding, territorial defense, predator detection). If weather conditions were unfavorable enough to seriously interfere with these activities, the animals returned to their burrows. If, however, conditions were less than ideal but not sufficient to force them into burrows, the squirrels may have responded with slight modifications of (1) the frequency of some behaviors or (2) posture. For example, on cold, sunny days the squirrels used postures that maximized their heat gain from the sun, whereas on hot, sunny days they used postures that minimized heat gain from the sun (Zegers 1977). In general, activity level (i.e., number of individuals above ground at any one time) decreased during cool and cloudy periods and during hot and sunny periods. Likewise Baudinette (1972) found that the California ground squirrel, *S. beecheyi*, avoided the warmest periods of summer days by remaining in the favorable environment of the burrow. The blacktail prairie dog, *Cynomys ludovicianus*, (Althen 1975) also showed peak activity above ground synchronous with times of optimal microenvironmental thermal conditions.

ACKNOWLEDGMENTS

Sigma Xi and the Kathy Lichty Memorial Fund of the University of Colorado provided financial support. Dr. Olwen Williams gave valuable suggestions and guidance. Dr. Steven Telleen helped with some of the field work. Thanks to James Ha, Drs. J. F. Merriitt, D. McCracken, and S. Ha and two anonymous reviewers for their helpful suggestions concerning this manuscript.

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A NEW PULVINATE *ERIOGONUM* (POLYGONACEAE) FROM UTAH¹

James L. Reveal²

ABSTRACT.— A new species of pulvinate wild buckwheat, *Eriogonum soredium* (Polygonaceae, Eriogonoideae) is described from near-barren limestone slopes in the Grampian Hill area near Frisco, Beaver County, Utah. The new species is outwardly similar to *E. shockleyi* S. Wats. but may be readily distinguished by its glabrous (not pubescent) flowers and fruits, generally smaller leaves, more numerous involucre per head, turbinate (not campanulate) involucre with 5, rarely 4 (not 5 to 10) teeth, and the smaller flowers.

Botanical explorations in the Intermountain Region as part of the general survey for rare and restricted vascular plants continue to reveal new, localized species heretofore unknown. The present discovery represents one of many new species to be found by Dr. Stanley L. Welsh of Brigham Young University and those associated with his investigations of the endangered and threatened flora of Utah.

Eriogonum soredium Reveal, sp. nov. A *E. shockleyi* floribus et fructibus glabris differt.

Low, matted herbaceous perennial with numerous dense rosettes of leaves forming a dense, compact mat 1–3 dm across, the caudex with numerous branches, the upper portion densely matted with persistent leaves and petiole-bases, arising from a stout, woody taproot; *leaves* clustered, persistent, forming tight, compact rosettes of numerous leaves, the leaf-blade narrowly elliptic to narrowly oblong, (2) 2.5–4.5 (5) mm long, (0.7) 1–1.8 (2) mm wide, densely whitish-tomentose on both surfaces, the apex blunt and rounded or sometimes broadly acute, the base cuneate, the margin entire, rolled and thickened but not revolute, the petiole short, 0.5–2 (3) mm long, densely white-tomentose, the petiole-base narrowly elongated, (0.5) 1–3 mm long, 0.4–0.5 mm wide, densely white-tomentose without, glabrous and tannish within; *flowering stems* erect or nearly so, scapose, 2–8 mm long, tomentose in anthesis but becoming less so at maturity; *inflorescences* capitate, the head 4–8 mm across; *bracts* 6–8, lanceolate

to narrowly triangular, 1.3–1.6 (1.8) mm long, tomentose without, glabrous within, distinct and not at all fused basally; *involucre* 4–6 per head, turbinate, 2 mm long, 1.3–1.5 mm wide, densely tomentose without with long tangled white hairs especially along the teeth and margin of the tube, glabrous within except for along the very margin, the (4) 5 erect, triangular and acute teeth 0.5–0.6 mm long, with a well-defined hyaline but pubescent membrane between each tooth, the bractlet linear-oblongate, 2–2.5 mm long, densely pubescent, especially apically, with long tangled hairs, less pubescent and with shorter gland-tipped hairs below, the pedicel long, 2–2.5 (3) mm long, glabrous; *flowers* white with reddish bases and midribs, (1.5) 2–2.5 mm long, glabrous without, sparsely glandular especially along the midrib within, the tepals slightly dimorphic, those of the outer whorl broadly obovate, 2.5–3 mm long and 1.6–2 mm wide when flattened, mostly spreading to recurved in anthesis and fruit, the apex broadly rounded and often emarginate, those of the inner whorl narrowly obovate, 2 mm long and 1.5 mm wide when flattened, mostly spreading in anthesis and fruit, the apex broadly rounded to truncate and often emarginate, united up to ¼ their length, the base rounded or nearly so, the lower portion of the midrib keeled in late anthesis and fruit; *stamens* slightly included, the filament 2.5–3 mm long, very sparsely pubescent basally, the anther reddish, oval, 0.4–0.5 mm long; *achenes* light brown, glabrous, 2–2.5

¹Work on this study has been supported by National Science Foundation Grant BMS75-13063. This is Scientific Article A2992, Contribution No. 5980, Maryland Agricultural Experiment Station, Department of Botany.

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mm long, the narrowly globose base tapering to a long, 3-angled beak (Fig. 1).

TYPE.—UTAH: Beaver Co., Grampian Hill, San Francisco Mts., near Frisco, on limestone hill S of rd just past turnoff to pass, sec. 23, T.27S., R.13W., 6600 ft elev., 29 Aug 1980, *Welsh, Chatterley & Anderson 20192*. Holotype, US. Isotypes, BRY, MARY, and 9 to be distributed from BRY.

ADDITIONAL SPECIMENS EXAMINED.—UTAH: Beaver Co., Frisco, sec. 23, T.27S., R.13W., 7300 ft elev., 6 Jun 1978, *Ostler & Anderson 1261* (BRY); San Francisco Mts., sec. 33, T.26S., R.13W., 14 June 1978, *Ostler & Anderson 1350* (BRY); Grampian Hill, sec. 23, T.27S., R.13W., 6740 ft elev., 25 June 1980, *Welsh & Chatterley 19653* (BRY, MARY).

Eriogonum soredium (from the Greek *soredium* meaning “small heap” alluding to the mat-forming habit of the plant) is most closely related to *E. shockleyi* S. Wats., a widespread Intermountain Region species which ranges from eastern California to western Colorado and northwestern New Mexico, and from the Snake River Plains of southern Idaho to northern Arizona. The new species differs from *E. shockleyi* most markedly in its glabrous flowers and fruits, but in addition the new species may be recognized by its smaller and generally narrower leaves (2–5 mm long in *E. soredium* versus 2–12 mm long in *E. shockleyi*), more numerous involucre (4 to 6 instead of 2 to 4) per head, its turbinate (not campanulate) involucre with 4 or 5 teeth rather than 5 to 10 as in *E. shockleyi*, and the



Fig. 1. *Eriogonum soredium*: A, habit of growth; B, involucre; C, leaves and involucre; D, flowers.

smaller flowers (up to 2.5 mm long in *E. soredium*, up to 4 mm long in *E. shockleyi*). In terms of habit the two are similar: both form rather compact mats of numerous, densely leaved rosettes. The flower color of *E. shockleyi* is more a creamy-white than the pure white of *E. soredium*, although the former may have yellowish flowers as well.

In my treatment of *Eriogonum* for Utah (Reveal, 1972), *E. soredium* will key (page 175) to *E. panguicense*. Here the dichotomy may be changed accordingly:

- EE. Flowers white.
- F. Stems glabrous, 0.2–30 cm long; involucre glabrous; mountains of Sevier Co. southward to Kane and Washington cos. 37. *E. panguicense*
- FF. Stems tomentose, up to 0.8 cm long; involucre tomentose; low hills near Frisco, Beaver Co. 39a. *E. soredium*

The new species is local and rare and occurs near populations of *Eriogonum shockleyi*. The Frisco area is noted for its historic mining operations, and for this reason *E. soredium* must be regarded as a potentially threatened species of flowering plants.

ACKNOWLEDGMENTS

I am grateful to Stanley L. Welsh for obtaining specimens of this new species so that it might be characterized. The illustration is by Kaye H. Thorne of Brigham Young University's Herbarium; I appreciate her efforts.

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A CHECKLIST OF THE ALPINE VASCULAR FLORA OF THE TETON RANGE, WYOMING, WITH NOTES ON BIOLOGY AND HABITAT PREFERENCES

John R. Spence^{1,2} and Richard J. Shaw¹

ABSTRACT.— A checklist of the vascular flora of the alpine zone (treeless vegetation above 9500 feet or 2900 m) of the Teton Range is presented. For each of the 216 species, six attributes are listed: flower color and shape, pollination mode, life form, habitat preference, and whether each species is found in the Arctic. White and yellow flowered species are most common, and zoophilous species greatly predominate over anemophilous and apomictic species. Perennial/biennial herbs are the most common life form. Common habitats in the alpine zone include dry and wet meadows, bogs, debris accumulations, and cliffs and rock faces. Arctic species account for 25.9 percent of the flora. The 216 species are distributed among 111 genera and 36 families. The largest families, in order of size, are Asteraceae, Poaceae, Cyperaceae, Brassicaceae, Rosaceae, and Scrophulariaceae.

The Teton Range, located for the most part inside Grand Teton National Park, is a typical fault block range. The mountains are about 60 km long and average 6 to 9 km wide. The major peaks in the center of the range and to the north are composed of Precambrian gneisses, schists, and granites. The southern peaks are capped by Paleozoic sedimentary rocks, and the divide to the west of the main peaks consists of Paleozoic and Mesozoic rocks. The range has been extensively glaciated in the past, and several small cirque glaciers of the Neoglacial age exist in sheltered areas of the range (Love and Reed 1968, Reed and Zartman 1973). The climate on the floor of Jackson Hole to the east of the Tetons is continental, with long, cold winters and a short growing season. Annual mean temperature is low. Precipitation is also low, falling mostly as snow in the winter months (Reed 1952, Shaw 1958).

The vascular flora of the Tetons has been well documented over the last 30 years (Shaw 1958, 1968, 1976). Approximately 150 species were listed as occurring in the alpine zone (Shaw 1976, unpublished data). Recent intensive collecting in portions of the alpine zone (Spence 1980) and reexamination of herbarium collections (Hartman and Lichvar 1979) have added more than 50 additional species.

The purposes of this checklist are to include all the recent information on the alpine

flora of the Teton Range and provide general information on floral characteristics, pollination modes, and habitats in the alpine zone. Phytogeographical relationships will also be mentioned. In this paper, the alpine zone is defined as high elevation areas of treeless vegetation, with the lower limits arbitrarily set at 9500 feet (2900 m). Although timberline (composed of *Pinus albicaulis*, *Picea engelmannii*, and *Abies lasiocarpa*) is generally found at elevations of 10,000 to 10,500 feet (3050 to 3200 m) in the Tetons, many areas below this support typical alpine species. Such areas include many of the cirques in the range, and the neoglacial deposits below the present glaciers.

METHODS

The checklist was collected from studies by Merkle (1962, 1963), Scott (1966), Shaw (1976), Spence (1980), and Hartman and Lichvar (1979), supplemented by personal observations and herbarium materials. All species on the list can be found on deposit at the Intermountain Herbarium (UTC) at Utah State University, the Rocky Mountain Herbarium (RM) at the University of Wyoming, and the Moose Herbarium in Grand Teton National Park. Polunin (1959) and Hultén (1968) were consulted for those species found in the Arctic. For each species six characteristics are noted. An asterisk (*) before the name of the species indicates it is found in

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the Arctic; a dagger (†) indicates the species is characteristically subalpine. Flower color is listed as w = white, y = yellow, v = violet, p = pink, b = blue, r = red, br = brown, g = green, and o = orange. Only species with conspicuously colored flowers are indicated. Flower shape is listed as a = actinomorphic, z = zygomorphic, and is listed only for those species with conspicuously colored flowers. Pollination mode is listed as Z = zoophilous, A = anemophilous or apomictic. Fryxell (1957), Pojar (1974), Ostler and Harper (1978), and Swales (1979) were consulted for aid in determining pollination mode. Life form is listed as s = shrub, p = perennial/biennial herb, g = perennial/biennial graminoid, and a / annual herb or graminoid. Major habitat types are listed as 1 = dry meadows, 2 = wet meadows, 3 = bogs, 4 = debris accumulations, 5 = cliffs and rock faces, 6 = neoglacial deposits. For more information on the habitat types see the discussion and Table 3.

RESULTS AND DISCUSSION

Table 1 lists the 216 species of vascular plants and presents for each species the biological attributes and habitat preferences by family in alphabetical order within the major categories Ferns, Fern Allies, and Gymnosperms; Dicots; and Monocots. The species are arranged in alphabetical order within each family. Table 2 is a statistical summary of the species and their attributes.

More than 50 percent of the species belong to the six largest families. In addition, 78 of the species belong to the 11 largest genera. It is interesting to note that the six families listed in Table 2 are also the six largest families in the flora of Teton County (Shaw 1976). Indeed, the genera *Carex*, *Potentilla*, *Poa*, *Salix*, and *Erigeron* are also listed as being among the largest genera in Teton County.

White and yellow flowered species predominate (64.1 percent). This result is similar to data presented by Ostler and Harper (1978) in a study of plant communities in the Wasatch Mountains of Utah and Idaho. In that study, from 65 to 75 percent of all conspicuously colored flowers in several alpine communities were white or yellow. This is a common feature of alpine floras throughout

the world (Wardle 1978). One possible reason for the commonness of white and yellow flowers in the alpine zone could be that the most common and important pollinators often are generalist fly and bee species, which frequently prefer such colors (Percival 1965, Moldenke 1976, Wardle 1978).

Some difficulty was encountered with the category Pollination Mode. Table 2 shows that 75.2 percent of the species are characteristically animal pollinated. This should be considered as a maximum value, because many of the species included in this category are probably autogamous, especially in the Brassicaceae. Not enough information on breeding systems of alpine species is available yet to state definitely whether a species outcrosses or is predominantly autogamous. The category Anemophilous/Apomictic species includes most monocots, *Artemisia*, *Oxyria digyna*, and the known apomicts *Taraxacum officinale* and *Polygonum viviparum* (Fryxell 1957, Swales 1979). Some of the grasses, particularly the *Poa* species, are probably partially or wholly apomictic also.

In the category Arctic and Alpine species 56, or 25.9 percent, are included. This can be compared with the Beartooth Range 150 km to the north. There, 47 percent of the species occur in the arctic as well (Johnson and Billings 1962). The lower value for the Tetons is possibly due to the somewhat drier conditions found there compared with typical Rocky Mountain ranges like the Beartooths or the Wind River Range to the southeast (Mahaney 1980). The value of 25.9 percent is intermediate between the Beartooths and northern Great Basin Ranges to the southwest of the Tetons (Billings 1978). The somewhat drier conditions, perhaps accentuated during the Hypsithermal, probably explain the absence of such widespread arctic species as *Koenigia islandica*, *Gentiana algida*, and *Saxifraga caespitosa* in the Tetons. All three species occur in the Beartooth and Wind River Ranges (Johnson and Billings 1962, Scott 1966).

Certain species, such as *Senecio integerrimus*, *Carex douglasii*, *Mitella pentandra*, and *Eriophyllum lanatum*, are more characteristic of the subalpine zone in the Tetons. The inclusion of the 18 subalpine

TABLE 1. A list of all species occurring in the alpine zone of the Teton Range with flower color and shape, pollination mode, life form, habitat preference, and origin noted. * indicates an arctic species; † indicates a subalpine species. The attributes are listed as 1=flower color (y=yellow, w=white, v=violet, p=pink, b=blue, r=red, br=brown, g=green, and o=orange), 2=flower shape (a=actinomorphic, z=zygomorphic), 3=pollination mode (A=anemophilous or apomictic, Z=zoophilous), 4=life form (p=perennial/biennial herb, s=shrub, g=perennial/biennial graminoid, a=annual herb/graminoid), and 5=habitat (1=dry meadows, 2=wet meadows, 3=bogs, 4=debris accumulations, 5=cliffs and rock faces, 6=neoglacal deposits). For more detail see Methods.

Family	1	2	Attribute		
Ferns, fern allies, and gymnosperms					
CUPRESSACEAE					
* <i>Juniperus communis</i> L. var. <i>depressa</i> Pursh	-	-	A	s	6
LYCOPODIACEAE					
<i>Lycopodium selago</i> L.	-	-	-	p	5
POLYPODIACEAE					
* <i>Asplenium viride</i> Huds.	-	-	-	p	4
<i>Athyrium filix-femina</i> (L.) Roth	-	-	-	p	6
<i>Cryptogramma crispa</i> (L.) R.Br. ex Hook. var. <i>acrostichoides</i> (R.Br.) Clarke	-	-	-	p	4,6
* <i>Cystopteris fragilis</i> (L.) Bernh.	-	-	-	p	4,6
SELAGINELLACEAE					
<i>Selaginella densa</i> Rydb.	-	-	-	p	4,5,6
Dicots					
APIACEAE					
* <i>Bupleurum americanum</i> Coult. & Rose	y	a	Z	p	1,4
<i>Cymopterus hendersonii</i> (Coult. & Rose) Cronq.	y	a	Z	p	4,6
ASTERACEAE					
* <i>Achillea millefolium</i> L. ssp. <i>lanulosa</i> (Nutt.) Piper var. <i>alpicola</i> (Rydb.) Garrett	w	a	Z	p	1,4,6
† <i>Agoseris aurantiaca</i> (Hook.) Greene	o	a	Z	p	1,2
<i>A. glauca</i> (Pursh) Raf.	y	a	Z	p	1,6
† <i>Anaphalis margaritacea</i> (L.) Benth. & Hook.	w	a	Z	p	6
<i>Antennaria alpina</i> (L.) Gaertn. var. <i>media</i> (Greene) Jeps.	w	a	Z	p	1
<i>A. microphylla</i> Rydb.	w	a	Z	p	6
<i>A. umbrinella</i> Rydb.	w	a	Z	p	1,6
<i>Arnica latifolia</i> Bong.	y	a	Z	p	1,4,6
<i>A. longifolia</i> D.C. Eat.	y	a	Z	p	2,6
† <i>A. mollis</i> Hook.	y	a	Z	p	2
<i>Artemisia campestris</i> L. ssp. <i>borealis</i> (Pall.) Hall & Clements	-	-	A	s	1
* <i>A. frigida</i> Willd.	-	-	A	s	1
* <i>A. norvegica</i> Fries ssp. <i>saxatilis</i> (Bess.) Hall & Clements	-	-	A	s	4,6
<i>A. scopulorum</i> Gray	-	-	A	s	4
<i>Aster alpinus</i> (T. & G.) A. Gray var. <i>haydenii</i> (Porter) Cronq.	v	a	Z	p	1
<i>Chaenactis alpina</i> (Gray) M. E. Jones	p	a	Z	p	4,6
<i>Cirsium tweedyi</i> (Rydb.) Petr.	p	a	Z	p	6
* <i>Erigeron compositus</i> Pursh	v	a	Z	p	1,4,6
<i>E. leiomerus</i> Gray	v	a	Z	p	1,4,6
<i>E. peregrinus</i> (Pursh) Greene ssp. <i>callianthemus</i> (Greene) Cronq.	p	a	Z	p	2
<i>E. simplex</i> Greene	v	a	Z	p	1,4
<i>E. ursinus</i> D.C. Eat.	v	a	Z	p	1
† <i>Eriophyllum lanatum</i> (Pursh) Forbes var. <i>integrifolium</i> (Hook.) Smiley	y	a	Z	p	6
<i>Haplopappus acaulis</i> (Nutt.) Gray	y	a	Z	p	4,6
<i>H. suffruticosa</i> (Nutt.) Gray	y	a	Z	s	1

Table 1 continued.

Family	Attribute				
	1	2	3	4	5
<i>Hieracium gracile</i> Hook.	y	a	Z	p	2,6
<i>Hymenoxys grandiflora</i> (T. & G.) Parker	y	a	Z	p	1,4,6
<i>Senecio amplexans</i> Gray	y	a	Z	p	1,4
<i>S. canus</i> Hook.	y	a	Z	p	4
<i>S. crassulus</i> Gray	y	a	Z	p	2
<i>S. fremontii</i> T. & G.	y	a	Z	p	4,6
† <i>S. integerrimus</i> Nutt.	y	a	Z	p	6
† <i>S. streptanthifolius</i> Greene	y	a	Z	p	6
† <i>S. triangularis</i> Hook.	y	a	Z	p	2
<i>S. werneriaefolius</i> Gray	y	a	Z	p	6
* <i>Solidago multiradiata</i> Ait.	y	a	Z	p	1,4,6
* <i>Taraxacum lyratum</i> (Ledeb.) DC.	y	a	Z	p	1,4,6
<i>T. officinale</i> Weber	y	a	A	p	1,2,4,6
<i>Townsendia montana</i> Jones	v	a	Z	p	4,6
BORAGINACEAE					
<i>Eritrichium nanum</i> (Vill.) Schrad. var. <i>elongatum</i> (Rydb.) Cronq.	b	a	Z	p	1,4,6
<i>Mertensia ciliata</i> (James) G. Don	b	a	Z	p	2
<i>Myosotis sylvatica</i> Hoffm. var. <i>alpestris</i> (Schmidt) Koch.	b	a	Z	p	1,4
BRASSICACEAE					
<i>Arabis drummondii</i> A. Gray	v	a	Z	p	1
* <i>A. holboellii</i> Hornem.	v	a	Z	p	1
<i>A. lemmonii</i> S. Wats.	v	a	Z	p	4,6
<i>A. lyallii</i> S. Wats.	v	a	Z	p	1,6
<i>A. nuttallii</i> Robinson	w	a	Z	p	6
<i>Draba apiculata</i> Hitchc.	w	a	Z	p	1
* <i>D. aurea</i> Vahl.	y	a	Z	p	4,5,6
<i>D. crassa</i> Rydb.	y	a	Z	p	4
* <i>D. crassifolia</i> Graham	y	a	Z	a	1
<i>D. lonchocarpa</i> Rydb.	w	a	Z	p	4,5,6
<i>D. oligosperma</i> Hook.	y	a	Z	p	4
<i>D. ventosa</i> Gray	w	a	Z	p	4,5
<i>Erysimum asperum</i> (Nutt.) DC.	y	a	Z	p	6
<i>Physaria australis</i> (Pays.) Rollins	y	a	Z	p	4
* <i>Smelowskia calycina</i> C. A. Meyer var. <i>americana</i> (Regal & Herd) Drury & Rollins	w	a	Z	p	1,6
CAMPANULACEAE					
* <i>Campanula rotundifolia</i> L.	v	a	Z	p	1,4
CARYOPHYLLACEAE					
<i>Arenaria congesta</i> Nutt.	w	a	Z	p	4,6
<i>A. nuttallii</i> Pax.	w	a	Z	p	6
* <i>A. obtusiloba</i> (Rydb.) Fern	w	a	Z	p	1,4,6
* <i>Cerastium arvense</i> L.	w	a	Z	p	2
* <i>C. beeringianum</i> Cham. & Schlecht.	w	a	Z	p	4,6
* <i>Sagina saginoides</i> (L.) Karst.	w	a	Z	p	2,6
* <i>Silene acaulis</i> L.	p	a	Z	p	1,4,6
† <i>S. parryi</i> (Wats.) Hitchc. & Mag.	w	a	Z	p	6
<i>Stellaria umbellata</i> Turcz.	w	a	Z	p	2
CRASSULACEAE					
<i>Sedum debile</i> S. Wats.	y	a	Z	p	4,6
<i>Sedum lanceolatum</i> J. Torr.	y	a	Z	p	1,4,6
<i>S. rhodanthum</i> A. Gray	p	a	Z	p	2
* <i>S. rosea</i> (L.) Scop. ssp. <i>integrifolium</i> (Raf.) Hult.	v	a	Z	p	2,3
<i>S. stenopetalum</i> Pursh	y	a	Z	p	4,5

Table 1 continued.

Family	Attribute				
	1	2	3	4	5
ERICACEAE					
* <i>Arctostaphylos uva-ursi</i> (L.) Spreng.	w	a	Z	s	2,4
<i>Caultheria humifusa</i> (Grah.) Rydb.	w	a	Z	s	2
<i>Kalmia microphylla</i> (Hook.) Heller	p	a	Z	s	2,3
<i>Phyllodoce empetrifloris</i> (Sw.) D. Don	p	a	Z	s	2
<i>P. glanduliflora</i> (Hook.) Cov.	w	a	Z	s	2,4
<i>Vaccinium scoparium</i> Leib.	w	a	Z	s	6
FABACEAE					
<i>Astragalus kentrophyta</i> Gray var. <i>implexus</i> (Canby) Barneby	v	z	Z	p	1,6
* <i>Hedysarum boreale</i> Nutt.	p	z	Z	p	6
<i>H. occidentale</i> Greene	v	z	Z	p	1,4
* <i>Oxytropis campestris</i> (L.) DC.	w	z	Z	p	1,4
<i>O. deflexa</i> (Pall.) DC. var. <i>foliosa</i> Hook. Barneby	v	z	Z	p	1,4,6
GENTIANACEAE					
<i>Gentiana calycosa</i> Griseb.	b	a	Z	p	2,6
GROSSULARIACEAE					
<i>Ribes montigenum</i> McClatchie	p	a	Z	s	2,6
HYDROPHYLLACEAE					
<i>Phacelia hastata</i> Dougl. var. <i>alpina</i> (Rydb.) Cronq.	v	a	Z	p	4,6
<i>P. sericea</i> (Grah.) Gray	v	a	Z	p	1,4,6
HYPERICACEAE					
† <i>Hypericum formosum</i> H.B.K. var. <i>nortoniae</i> (Jones) Hitchc.	y	a	Z	p	6
LINACEAE					
* <i>Linum perenne</i> L. var. <i>lewisii</i> (Pursh) Eat. & Wright	b	a	Z	p	1
ONAGRACEAE					
* <i>Epilobium alpinum</i> L.	p	a	Z	p	1,4,6
* <i>E. latifolium</i> L.	p	a	Z	p	2,4,6
POLEMONIACEAE					
<i>Linanthus nuttallii</i> Gray	w	a	Z	p	1,4
<i>Phlox pulvinata</i> (Wherry) Cronq.	w	a	Z	p	4
* <i>Polemonium pulcherrimum</i> Hook.	b	a	Z	p	4
<i>P. viscosum</i> Nutt.	b	a	Z	p	4,6
POLYGONACEAE					
<i>Eriogonum ovalifolium</i> Nutt. var. <i>depressum</i> Blank.	w	a	Z	p	4,6
† <i>E. umbellatum</i> Torr. var. <i>subalpinum</i> (Greene) Jones	y	a	Z	p	4
* <i>Oxyria digyna</i> (L.) Hill	g	a	A	p	2,4,5,6
<i>Polygonum bistortoides</i> Pursh	w	a	Z	p	2,6
* <i>P. viviparum</i> L.	w	a	A	p	2
PORTULACAEAE					
<i>Claytonia lanceolata</i> Pursh	p	a	Z	p	2
<i>C. megarhiza</i> (Gray) Parry	p	a	Z	p	4
<i>Lewisia pygmaea</i> (Gray) Robins.	p	a	Z	p	4,6
<i>L. triphylla</i> (Wats.) Robins.	p	a	Z	p	4
<i>Spraguea umbellata</i> Torr.	w	a	Z	p	4
PRIMULACEAE					
* <i>Androsace septentrionalis</i> L.	w	a	Z	a	1,6
<i>Dodecatheon conjugens</i> Greene	p	a	Z	p	2
<i>D. pulchellum</i> (Raf.) Merrill	p	a	Z	p	2
<i>Primula parryi</i> A. Gray	p	a	Z	p	2,4,5

Table 1 continued.

Family	Attribute				
	1	2	3	4	5
PYROLACEAE					
<i>Pyrola dentata</i> Smith	w	a	Z	p	4
* <i>P. minor</i> L.	p	a	Z	p	2,3
RANUNCULACEAE					
<i>Anemone multifida</i> Poir. var. <i>tetonensis</i> (Porter) Hitchc.	y	a	Z	p	1,6
<i>Aquilegia flavescens</i> S. Wats.	y	a	Z	p	2,4,6
<i>Caltha leptosepala</i> DC.	w	a	Z	p	2
<i>Ranunculus eschscholtzii</i> Schlecht.	y	a	Z	p	2
var. <i>alpinus</i> (Wats.) C. L. Hitchc.					
var. <i>eschscholtzii</i>					
var. <i>suksdorfii</i> (Gray) Benson					
<i>Trollius laxus</i> Salisb.	y	a	Z	p	2
ROSACEAE					
* <i>Dryas octopetala</i> L. var. <i>angustifolia</i> C. L. Hitchc.	w	a	Z	s	4
* <i>Geum rossii</i> (R. Br.) Ser. var. <i>turbinatum</i> (Rydb.) C. L. Hitchc.	y	a	Z	p	4
<i>Ivesia gordonii</i> (Hook.) T. & G.	y	a	Z	p	1,4
<i>Potentilla brevifolia</i> Nutt. ex T. & G.	y	a	Z	p	4
<i>P. concinna</i> Rich. var. <i>rubripes</i> (Rydb.) C. L. Hitchc.	y	a	Z	p	4
<i>P. diversifolia</i> Lehm.	y	a	Z	p	1,4
<i>P. flabellifolia</i> Hook.	y	a	Z	p	2
* <i>P. fruticosa</i> L.	y	a	Z	s	1,4,6
<i>P. glandulosa</i> Lindl. var. <i>pseudorupestris</i> (Rydb.) Breit.	y	a	Z	p	6
<i>P. gracilis</i> Dougl.	y	a	Z	p	2,6
* <i>P. nivea</i> L.	y	a	Z	p	2,4,6
<i>Rubus idaeus</i> L. ssp. <i>sachalinensis</i> (Levl.) Focke	w	a	Z	p	4
* <i>Sibbaldia procumbens</i> L.	y	a	Z	s	2,4,6
RUBIACEAE					
<i>Kellogia galioides</i> Torr.	w	a	Z	p	5
SALICACEAE					
* <i>Salix arctica</i> Pall.	-	-	Z	s	1,4,6
<i>S. cascadenis</i> Cockerell	-	-	Z	s	1,2,4
* <i>S. glauca</i> L.	-	-	Z	s	1,2
* <i>S. reticulata</i> L. ssp. <i>nivalis</i> (Hook.) Love et al.	-	-	Z	s	2
* <i>S. rotundifolia</i> L. ssp. <i>dodgeana</i> (Rydb.) Argus	-	-	Z	s	1,4
SAXIFRAGACEAE					
† <i>Mitella pentandra</i> Hook.	g	a	Z	p	2
<i>Parnassia palustris</i> L. var. <i>montanensis</i> (Fern & Rydb.) C. L. Hitchc.	w	a	Z	p	2
<i>Saxifraga adscendens</i> L.	w	a	Z	p	2,5
* <i>S. bronchialis</i> L. var. <i>austromontana</i> (Wieg.) Jones	w	a	Z	p	2,4,5,6
<i>S. debilis</i> Engelm.	w	a	Z	p	6
* <i>S. flagellaris</i> Willd.	w	a	Z	p	2,4,5
* <i>S. oppositifolia</i> L.	v	a	Z	p	2,4
<i>S. rhomboidea</i> Greene	w	a	Z	p	2,6
<i>Telesonix jamesii</i> (Torr.) Raf. var. <i>heucheriformis</i> (Rydb.) Bacigalupi	w	a	Z	p	4,5,6
SCROPHULARIACEAE					
<i>Bessya wyomingensis</i> (A. Nels.) Rydb.	v	z	Z	p	1
† <i>Castilleja miniata</i> Dougl.	r	z	Z	p	2,6
<i>C. pulchella</i> Rydb.	r	z	Z	p	1,2
<i>C. sulphurea</i> Rydb.	y	z	Z	p	1
<i>Mimulus lewisii</i> Pursh	p	z	Z	p	2,6

Table 1 continued.

Family	Attribute				
	1	2	3	4	5
<i>Pedicularis bractcosa</i> Benth.	y	z	Z	p	4
<i>P. contorta</i> Benth.	w	z	Z	p	1
* <i>P. groenlandica</i> Retz.	v	z	Z	p	2,3
<i>P. parryi</i> Gray var. <i>purpurea</i> Parry	w	z	Z	p	1
† <i>Penstemon attenuatus</i> Dougl. ssp. <i>pseudoprocerus</i> (Rydb.) Keck.	b	z	Z	p	6
<i>P. montanus</i> Greene	v	z	Z	p	4
<i>P. whippleanus</i> Gray	y	z	Z	p	1,4,6
* <i>Veronica wormskjoldii</i> Roem. & Schult.	v	z	Z	p	2,6
VALERIANACEAE					
<i>Valeriana acutiloba</i> Rydb.	w	a	Z	p	1,4
VIOLACEAE					
<i>Viola adunca</i> J. E. Smith	v	z	Z	p	2
Monocots					
CYPERACEAE					
<i>Carex albonigra</i> MacKenz.	-	-	A	g	4,6
* <i>C. atrata</i> L.	-	-	A	g	1,2
† <i>C. douglasii</i> Boott.	-	-	A	g	6
<i>C. elynoides</i> Holm	-	-	A	g	1,4,6
† <i>C. geyeri</i> Boott.	-	-	A	g	1
<i>C. haydeniana</i> Olney	-	-	A	g	1,4,6
† <i>C. illota</i> Bailey	-	-	A	g	2,3
<i>C. luzulina</i> Olney	-	-	A	g	6
<i>C. microptera</i> Mack.	-	-	A	g	1,4
<i>C. nardina</i> Fries	-	-	A	g	1,2
<i>C. nigricans</i> C. A. Mey.	-	-	A	g	1,2
<i>C. nova</i> L. Bailey	-	-	A	g	2,6
<i>C. paysonis</i> Clokey	-	-	A	g	6
<i>C. phacocephala</i> Piper	-	-	A	g	4,6
<i>C. pyrenaica</i> Wahl.	-	-	A	g	1,2,4
† <i>C. rossii</i> Boott.	-	-	A	g	1,2
JUNCACEAE					
<i>Juncus drummondii</i> E. Bey.	-	-	A	g	2,6
<i>J. mertensianus</i> Bong.	-	-	A	g	2,3,6
<i>J. parryi</i> Engelm.	-	-	A	g	1,2,4
<i>Luzula piperi</i> (Cov.) Jones	-	-	A	g	2,3,6
* <i>L. spicata</i> (L.) DC.	-	-	A	g	2,4,6
LILIACEAE					
<i>Erythronium grandiflorum</i> Pursh	y	a	Z	p	2
* <i>Lloydia scrotina</i> (L.) Sweet.	w	a	Z	p	1,4
* <i>Zigadenus elegans</i> Pursh	w	a	Z	p	2
<i>Tofieldia glutinosa</i> (Michx.) Pers.	w	a	Z	p	2
POACEAE					
<i>Agropyron caninum</i> (L.) Beauv. var. <i>latiglume</i> (Scribn. & Smith) Hitchc.	-	-	A	g	1,4,6
var. <i>andinum</i> (Scribn. & Smith) Hitchc.	-	-	A	g	1,4,6
<i>A. scribneri</i> Vasey	-	-	A	g	2
<i>Agrostis humilis</i> Vasey	-	-	A	g	6
† <i>A. idahoensis</i> Nash	-	-	A	g	1,2
* <i>A. scabra</i> Willd.	-	-	A	g	2,3
<i>A. thurberiana</i> Hitchc.	-	-	A	g	1,4
<i>A. variabilis</i> Rydb.	-	-	A	g	4,6
* <i>Calamagrostis purpurascens</i> R. Br.	-	-	A	g	

Table 1 continued.

Family	Attribute				
	1	2	3	4	5
<i>Danthonia intermedia</i> Vasey	-	-	A	g	1,4
<i>Deschampsia atropurpurea</i> (Wahl.) Scheele	-	-	A	g	2
* <i>D. cespitosa</i> (L.) Beauv.	-	-	A	g	2
* <i>Festuca ovina</i> L.	-	-	A	g	1,6
<i>Leucopoa kingii</i> (Wats.) Weber	-	-	A	g	1,6
* <i>Phleum alpinum</i> L.	-	-	A	g	2,3,4,6
<i>Poa alpina</i> L.	-	-	A	g	1,4,6
<i>P. cusickii</i> Vasey var. <i>cusickii</i> Hitchc.	-	-	A	g	4
var. <i>epilis</i> (Scribn.) Hitchc.					
<i>P. incurva</i> Scribn. & Wms.	-	-	A	g	4
<i>P. nervosa</i> (Hook.) Vasey var. <i>wheeleri</i> (Vasey) Hitchc.	-	-	A	g	1,4
<i>P. pattersonii</i> Vasey	-	-	A	g	1,4,6
<i>P. reflexa</i> Vasey & Scribn.	-	-	A	g	2
<i>P. rupicola</i> Nash ex Rydb.	-	-	A	g	4
<i>P. sandbergii</i> Vasey	-	-	A	g	6
* <i>Trisetum spicatum</i> (L.) Richt.	-	-	A	g	1,2,4,6

species reflects their occasional appearance above timberline, generally in the glacial cirques.

The Tetons are quite high, with 55 peaks and 7 percent of the area of the park above 10,000 feet (3050 m). Despite this, probably because the range is so precipitous, extensive stretches of alpine meadow vegetation are uncommon. Nevertheless, some extensive areas of alpine meadows can be found in the northern part of the range (e.g., Moose Basin), around Schoolroom Glacier to the west of the main peaks, in Alaska Basin, and along the Skyline Trail in the southern part of the range. Taluses and other debris accumulations, on the other hand, are abundant throughout the range and are probably the most widespread and common alpine habitats.

The major habitat types in which each species is commonly found are listed in Table 1. Although many species are characteristic of a particular habitat, other species can be found in a variety of habitats. For this reason the assignment of each species to a particular habitat or habitats should be interpreted only in a broad sense. For some species, the habitat preference is only tentative. As more information becomes available on habitat preferences and vegetation ecology in the alpine zone of the Tetons, it is hoped that a more rigorous and exact classification will be produced. Table 3 presents the major habitat types in the alpine zone using physical and

vegetative characteristics. A brief discussion of each habitat and some of the characteristic species of each follows.

Lakes and streams are common in the alpine zone of the Tetons, but no aquatics have been found. Since Scott (1966) listed a collection of *Ranunculus natans* from the alpine of the Beartooth Range, this species should be sought in the alpine of the Tetons.

Bogs, where found, generally occur close to the lower limits of the alpine zone at 9500 feet (2900 m). They commonly occur in cirques and local depressions in the major canyons, especially along streams. Mosses are common, and *Carex* and *Salix* species dominate the vascular flora. Other species found in bogs include *Pedicularis groenlandica*, *Pyrola minor*, *Sedum rosea*, *Kalmia microphylla*, and *Agrostis thurberiana*.

The bog habitat usually grades into wet meadow habitat, with any boundary between the two often difficult to find. The wet meadow habitat is common at lower elevations, particularly in cirques, around lakes and seeps, and along streams. Vegetation occurring below late-lying snowbanks is also included in this habitat type. Wet meadows are usually dominated by various Ranunculaceae (especially *Caltha leptosepala*), and *Polygonum bistortoides*, *Pedicularis groenlandica*, *Veronica wormskjoldii*, *Deschampsia cespitosa*, and *Carex*, *Potentilla* and *Salix* species. Along streams *Phyllodoce empetriformis* and *P. glanduliflora* are especially common, along

with *Epilobium latifolium*, and *Carex*, *Dodecatheon*, and *Castilleja* species. Seeps generally support a rich mixture of *Mertensia ciliata*, and *Carex*, *Mimulus*, and *Saxifraga* species, with many mosses. Ground which is exposed late by late melting snow usually supports species like *Claytonia lanceolata*, *Erythronium grandiflorum*, and *Ranunculus eschscholtzii*.

Dry meadows are fairly common. Areas like Alaska Basin, parts of Moose Basin, large

stretches along the Skyline Trail in the southern Tetons, and slopes in the major cirques consist of this habitat type. At high elevations, this habitat is composed of scattered patches of plants with many bare areas between the patches. The top of Prospectors Mountain and Hurricane Pass are good examples of this type of vegetation. The lower elevation and more extensively vegetated dry meadows are dominated by species of the Asteraceae and Poaceae families. *Astragalus*

TABLE 2. Statistical summary of the alpine flora of the Teton Range. The families with more than 10 species and the genera with 5 or more species are also listed.

Attribute	Number of species	Percent of total
LIFE FORM		
perennial/biennial herb	149	69.0
perennial/biennial graminoid	44	20.4
shrub	21	9.9
annual herb or graminoid	2	1.0
Total	216	100.0
FLOWER COLOR		
yellow	52	33.3
white	48	30.8
violet	23	14.7
pink	20	12.8
blue	8	5.1
red	2	1.3
brown/green/orange	3	2.0
Total	156	100.0
FLOWER SHAPE		
actinomorphic	137	87.8
zygomorphic	19	12.2
Total	156	100.0
POLLINATION MODE		
zoophilous	158	75.2
anemophilous/apomictic	52	24.8
Total	210	100.0
ORIGIN		
alpine but not arctic	142	65.7
arctic and alpine	56	25.9
subalpine	18	8.4
Total	216	100.0
NUMBER OF FAMILIES	36	—
NUMBER OF GENERA	111	—
NUMBER OF SPECIES	216	—
LARGEST FAMILIES (number of species)		LARGEST GENERA (number of species)
Asteraceae (39)	<i>Carex</i> (16)	<i>Agrostis</i> (5)
Poaceae (23)	<i>Poa</i> (8)	<i>Arabis</i> (5)
Cyperaceae (16)	<i>Potentilla</i> (8)	<i>Erigeron</i> (5)
Brassicaceae (15)	<i>Senecio</i> (8)	<i>Salix</i> (5)
Rosaceae (13)	<i>Draba</i> (7)	<i>Sedum</i> (5)
Scrophulariaceae (13)	<i>Saxifraga</i> (6)	

kentrophyta, *Carex nigricans*, and *Juncus drummondii* are also very common. At high elevations the vegetation is dominated by *Hymenoxys grandiflora*, *Smelowskia calycina*, *Oxytropis campestris*, *Lloydia serotina*, and *Eritrichium nanum*.

Debris accumulations include taluses, scree slopes, and boulder fellfields. These habitats are often physically disturbed by mass movements. Vegetation cover is usually very low. Many species have adapted to the disturbed and often xeric conditions of debris accumulations, generally by producing extensive root or rhizome systems. Common species include *Dryas octopetala*, *Oxyria digyna*, *Cryptogramma crispa*, *Senecio fremontii*, *Phacelia hastata*, *Erigeron compositus*, *Senecio longifolia*, and *Epilobium alpinum*.

Neoglacial deposits include the full range of debris accumulations, plus some unique minor habitat types (Spence 1980). Characteristic species include *Oxyria digyna*, *Senecio fremontii*, *Poa pattersonii*, *Juncus drummondii*, *Carex phaeocephala*, and *Trisetum spicatum*. Floristically, Neoglacial deposits

are among the richest of the habitat types in the alpine of the Tetons.

Rock faces and cliffs are abundant in the Tetons. The most common species found in this habitat type include *Telesonix jamesii*, *Oxyria digyna*, and various species of *Saxifraga*, *Arabis*, and *Draba*.

ACKNOWLEDGMENTS

Ivan G. Palmblad and David R. Given read and criticized an early draft of the manuscript.

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TABLE 3. The major habitat types in the alpine zone of the Teton Range, with some physical and vegetative characteristics noted for each type.

Habitat type	Characteristics
Lake and stream habitat	standing or moving water present.
Bog habitat	water-saturated soil throughout the growing season, sometimes flooded in early season, vegetation cover usually 100 percent, with mosses common.
Wet meadow habitat	ground flat to gently sloping, soil generally moist, obvious boulders few and scattered, usually occurs near streams, lakes, seeps, bogs, or late lying snowbanks, vegetation cover generally high (often 100 percent), usually found below 10,500 ft (3200 m).
Dry meadow habitat	ground flat to gently sloping, soil generally dry, obvious boulders few and scattered, usually occurs away from lakes, streams, seeps, bogs, or late lying snowbanks, vegetation cover moderate to high at low elevations, low at high elevations.
Debris accumulation habitat	ground flat to steeply sloping, little soil, mostly accumulations of moderate- to large-sized rock fragments, vegetation cover very low, plants usually confined to crevices between rocks.
Rock face and cliff habitat	mostly bedrock, generally steep (40° +) sometimes with ephemeral streams in early season, plants usually growing on small ledges or in cracks in the rocks.
Neoglacial deposits	flat to more often steep accumulations of glacial debris, usually near existing glaciers or permanent snowbanks, vegetation cover generally low, recently formed (100-3000 years old). See Benedict 1973, Mahaney 1975.

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SOME SPATIAL AND BEHAVIORAL FEATURES OF THE THIRTEEN-LINED GROUND SQUIRREL

Tim W. Clark¹

ABSTRACT.— Some relationships between home range, agonistic behavior, and reproductive patterns in thirteen-lined ground squirrels were investigated in Laramie Plains, Wyoming (August 1966–April 1969). Population size and densities fluctuated seasonally and annually. Adult male ($N = 7$) home ranges averaged 0.24 ha and were smaller than those of the female ($N = 9$), which averaged 0.35 ha. Agonistic interactions were more frequent during the natal period (late May–June) than during the breeding-gestation period (mid April–May). Most squirrels (86 percent) shared capture sites and had overlapping home ranges. However, a certain degree of spacing existed because of agonistic behavior.

This study investigated the relationship between home range, agonistic behavior, and reproductive patterns in a natural population of thirteen-lined ground squirrels.

METHODS

A 10 ha grid with Sherman traps at 20 m intervals was live-trapped from August 1966 to April 1969. Captured squirrels were marked by toe clipping and dye marking with Nyanzol black fur dye. A grid of colored stakes at 30 m intervals was superimposed over the trap grid to facilitate squirrel observations. Home ranges (Dice 1952) and “centers-of-activity” (Hayne 1949) were determined. To the polygon-shaped home range, a boundary strip of one-half the distance between traps was added. Observations were made from two elevated blinds (4 m tall) and vehicles.

Reproductive patterns were estimated by examining males for testis position and females for perforated vagina, swollen vulva, and recent evidence of parturition or lactation (Packard 1968).

Agonistic data were collected in 1968 by observing marked and unmarked squirrels behaviorally interacting in a 2 ha sample area. Ten 1-hr observation sessions (0900–1000) were made five days apart. Five fell within the “breeding-gestation” period (15 April–5 May) and five in the “birth-natal” period

(1–31 June). Just prior and following each session, five scans were made of the study site to determine identifications of all active squirrels, their locations, and type of activities exhibited. Social interactions were classified as “agonistic” or “sexual” after Burns (1968). The “form” and “result” of all agonistic interactions was noted. The form was either “contact” (in which some physical contact occurred), “chase” (both squirrels moving at least 1 m in the same direction at same time), or both. Even though neither contact nor chase were involved, an interaction was still called agonistic if it contained “threat” postures (Grubitz 1966). Results were classified as “dominant,” “stand-off,” or “subordinant” (a squirrel spatially supplanted by a second squirrel).

STUDY AREA

Squirrels were studied on Hutton Lake National Wildlife Refuge, Albany County, Wyoming. This area is montane (elev 2400 m) and consists of native short grass prairie called “Transitional Life-Zone” by Cary (1917). Predominant plants included blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*), june grass (*Koeleria cristata*), needle grass (*Stipa* spp.) and prickly pear cactus (*Opuntia polyacantha*) (Clark 1971).

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RESULTS

In all, 196 squirrels were captured: 18 in 1966, 79 in 1967, 87 in 1968, and 12 in 1969. Squirrels emerged from hibernation from late March to early April and disappeared from mid-August to early October each year. Two general peaks in captured rates occurred (Fig. 1), the first during the breeding season and early gestation in late April and May and the second in early July when young squirrels made their initial appearance above ground.

By 1968, a large number of squirrels had been marked, allowing identification of age structure. Therefore, the 1968 data is felt to be most representative and is given below. Density peaks in 1968 corresponded to population peaks, when 15.2 animals per ha were present during breeding and early gestation and 12.7 when young first appeared above ground. The mean density from 31 March to 17 August 1968, was 4.0 per ha.

Age and sex structure varied seasonally. From late March to July, the population was

comprised of 1+ yr olds. By mid-September the entire aboveground population consisted of young of the year. In August 1968, the population was 28.6 percent young of the year (14M:6F), 60.0 percent adults of unknown age (18M:4F), and 11.4 percent adults 2+ yrs old (4M:4F). The sex ratio was 1.0M:0.4F for young, 1.0M:1.3F for adults (age unknown), and 1.0M:1.0F for squirrels 2+ yrs old. There were nearly twice as many males as females in the young age class, but this changed in favor of females in the adult age class.

The 1968 mean trapping success per 100 trap days was 7.1 (range 1.6–20.1). Mean number of captures per squirrel was 4.0. About 36.1 percent of the squirrels captured were caught only once, 21 percent twice, 16 percent 3 or 4 times, 18 percent 5 to 10 times, and 8 percent 11 or more times.

Home range size varied between sexes. Adult females' home ranges averaged about 40 percent larger than adult males. The mean number of times each adult male ($N=7$) was

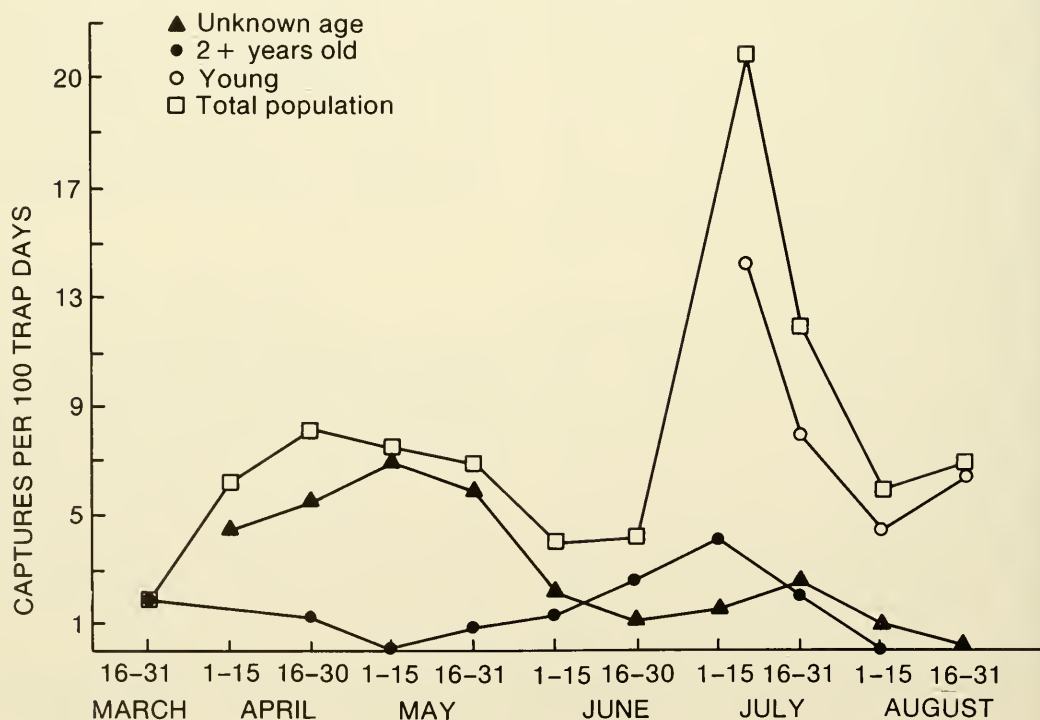


Fig. 1. Captures per 100 trap days expressed biweekly throughout the 1968 trapping period as an index of population activity.

captured or observed was $9.8 \text{ SD} \pm 2.1$; for each adult female ($N=9$) it was 16.6 ± 3.9 . Mean home range for adult males was $0.24 \text{ SD} \pm 0.11 \text{ ha}$ (range $0.11\text{--}0.39$); for adult females it was $0.35 \text{ SD} \pm 0.19$ (range $0.27\text{--}0.56$).

Breeding occurred in April (Table 1), a fact determined by examining the sexual condition of 69 squirrels. Young squirrels first appeared above ground in early July. By first counting backwards, using known nest confinement and gestation periods (Asdell 1946), then observing breeding in the field, we estimated the duration of these life history stages.

Agonistic behavior observations were expressed for two periods: breeding-gestation (mid-April–May) and natal care (late May–June). From 28 April to 4 May 1968 there was a peak of activity. Four instances of "courtship" behavior were noted that followed descriptions given by McCarley (1966) and Wistrand (1974). No copulatory behavior was seen. During this week 14 squirrels were later recaptured in areas up to 300 m away from their original capture sites. Mean capture success for 15 April to 31 May (breeding) was 6.9 per 100 trap days, more than twice the 3.1 capture index for the natal period (1–31 June). However, differences were not significant.

Of 29 agonistic interactions seen in 1968, 21 involved at least one female and 8 involved a male; the second animal in these interactions was not identified. Of agonistic interactions ($N=17$) observed during the natal period, 14 involved females. Table 2 gives the form of agonistic interactions seen. No

significant differences existed in the form of the interactions between the two periods.

Parturition burrows ($N=5$) were located by observing adult females carry mouthfuls of nest materials into certain burrows. These sites were taken as centers-of-activity. In males, geometric centers of home ranges were considered as centers-of-activity in 9 cases. Analyses of location and outcome of 24 agonistic interactions for these squirrels indicated that an individual tended to be dominant in interactions occurring nearest its center-of-activity (Table 3).

DISCUSSION

According to Kummer (1971), social affinity and spatial proximity are so highly correlated that the distribution of individuals in space can be used as first reading of the social structure. A great proportion (86 percent) of all squirrels in the study shared capture sites. By itself, a large overlap in capture sites does not necessarily indicate a large overlap in home range. Existence of agonistic interactions suggests that a portion of each home range was defended against intrusion, although this may have indicated hierarchy independent of actual geography. Nevertheless, a certain degree of spacing did exist as a result of agonistic behavior.

TABLE 2. "Form" of 29 agonistic interactions observed in thirteen-lined ground squirrels, Laramie Plains, Wyoming (1968).

Form	Breeding-gestation	Birth-natal
	1 April–31 May	1–31 June
Contact	2	4
Chase	4	3
Both	6	10
Totals	12	17

TABLE 1. Sexual condition of adult thirteen-lined ground squirrels in the Laramie Plains, Wyoming.

Sexual condition	Breeding-gestation	Birth-natal
	1 April–31 May	1–31 June
Females:		
Vulvae normal	1	8
Vulvae swollen and/or open	29	1
Lactating	1	9
Nonlactating	29	0
Males:		
Testes abdominal	1	3
Testes scrotal	25	1

TABLE 3. Results of 24 agonistic interactions in relation to distance from "centers-of-activity" in thirteen-lined ground squirrels.

Encounter results	Meters from center-of-activity		
	0–8	9–15	16+
Dominant	12	4	2
Stand-off	4	2	0
Subordinate	0	0	0
Totals	16	6	2

In a population of ground squirrels organized into overlapping home ranges, it can be assumed that few novel encounters between adults will occur once the basic home range configuration has been well established. This may account for the relatively few agonistic interactions seen in this study ($N=29$) and seen by Wistrand (1974), who saw only 19, compared to Grubitz (1966), who noted 767 in a closed area. Balph and Stokes (1963) suggested that, in Uinta ground squirrels, "territorial" behavior may be the result of an encroachment by one squirrel into the area of another squirrel's "individual distance" rather than a fixed site attachment. Wistrand (1974) considered that a similar pattern of agonistic behavior occurred in his thirteen-lined ground squirrel population.

Territorialism is suggested by squirrel's marked avoidance of certain burrows, especially during the natal period. In Richardson's ground squirrels, Yeaton (1972) noted that females possess a "territory" throughout the aboveground activity cycle. Wistrand (1974) noted that thirteen-lined ground squirrels defended burrows, but only at the time they occupied the burrow. He also noted that a burrow may be used by more than one squirrel, provided only one animal occupies it at a given time. A similar case may have existed in my study. Temporal-spatial mechanisms clearly need further elucidation before we understand thirteen-lined ground squirrel social organization.

ACKNOWLEDGMENTS

I thank Brent Costain, Don Streubel, Denise Casey, and Tom Campbell for critical advice on the manuscript. Rollin Denniston

provided encouragement. Cheryl Hughes drew the figures. The Marsh Fund of the National Academy of Sciences provided partial support for manuscript preparation.

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OVERWINTER SURVIVAL OF RING-NECKED PHEASANTS IN UTAH

Alan K. Wood¹ and Jack D. Brotherson²

ABSTRACT.— The influence of winter weather on the survival of Utah's ring-necked pheasants was evaluated using correlation analysis. This method used published Utah State Division of Wildlife Resources population data and a calculated winter warmth index. Results show four different patterns of survival occurring in the 14 counties analyzed.

Wagner and Stokes (1968) estimated overwinter survival of ring-necked pheasants (*Phasianus colchicus*) in Wisconsin. They correlated a fall population index with an overwinter survival index and with a spring population index. Their results suggested density independent winter survival for the statewide population. Perry (1946) proposed that severe winter weather in New York affected the vigor of pheasants but did not significantly increase overwinter mortality.

Edwards et al. (1964), Gates and Woehler (1968), and Gates (1971) suggest that harsh weather, particularly in late winter and early spring, may cause increased mortality of hens in the early summer during the brood-rearing season. Gates (1971) proposed that a decrease in body weight of hens caused by harsh winter weather delayed egg laying in spring and resulted in hens entering the breeding season in suboptimal physical condition. During the nesting and brood-rearing period, hens continue to lose weight; this results in reduced production of young and may lead to the death of the hen. Other studies have shown increased mortality due directly to winter storms, with rates reaching as high as 90 percent (Kimball et al. 1956). Evidence also indicates that predation rates increase with severity of winter weather (Dumke and Pils 1973). In this paper, population dynamics of ring-necked pheasants in Utah are evaluated using indices similar to those employed by Wagner and Stokes (1968) to determine the relationship of winter weather to survival.

METHODS

Data used in this analysis were compiled from Utah Upland Game Annual Reports from 1967 through 1979 (Nish 1967–1976, Bunnell and Olsen 1977–1978, Bunnell and Leatham 1979) and from Climatological Data of Utah (Mitchell 1962–1979). Preliminary models were derived for Box Elder, Cache, Duchesne, Sevier, Uintah, and Utah Counties to select indices for use in the final analyses.

The fall population index used was birds harvested per hunter day afield. In 1973 the daily bag limit on pheasants in Utah was lowered from three to two cocks per day. However, the mean harvest rate did not show a substantial decrease in response to this change. It appeared that reducing the bag limit did not influence hunter success. No attempt was made to adjust the fall index to the change in bag limit.

The summer index used was computed by subtracting young/km from total birds/km yielding an index of adult pheasants/km. These summer population data are collected each August along established census routes. Summer population data were used because spring population data were not available in Utah. Also, by using summer data we can incorporate summer mortality due to winter weather as discussed previously.

A winter survival index was calculated by dividing the summer index by the fall index of the previous year. All population indices

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were multiplied by 100 to give whole numbers.

In the preliminary models, a winter severity index utilizing temperature and precipitation variables similar to Gates' (1971) procedure was attempted, but no significant relationships were apparent between the survival index and the winter severity index. Precipitation alone showed no significant relationship to pheasant survival. There was, however, a significant positive correlation between winter (December, January, and February) temperature and the survival index. Hence, we hypothesized that for the areas of Utah studied, there was not enough precipitation during the winter months to significantly affect the pheasant numbers. Winter precipitation varied from only trace amounts in Emery County, to a high three-month total of 27.3 cm (10.75 inches) in Box Elder County. As a result of preliminary findings, a winter warmth index was used in this analysis, calculated by summing the average temperatures for December, January, and February only.

The fall population index was correlated with the log of the summer population index for the following year. The winter warmth index was correlated with the log of the appropriate survival index. Log transformations of the dependent variables were used because they yielded slightly higher correlation coefficients than analyses using raw data.

Areas analyzed were selected from throughout Utah. Counties were selected based on the completeness of their population data. Weather stations within the selected counties were selected based on their proximity to major pheasant-hunting areas and on the completeness of their climatological data (Table 1). Where monthly weather data were missing for any station, missing values were filled with appropriate monthly averages from 1962 through 1979. For stations with missing data for an entire year, values were estimated using data from a neighboring station.

RESULTS

The major pattern of population dynamics identified in this study showed a strong correlation between the fall and summer population

indices, with little or no influence of winter temperatures on survival (Table 2). This pattern was observed for Beaver, Box Elder, Juab, Salt Lake, Tooele, and Utah Counties. It implies that overwinter survival rates do not fluctuate radically from year to year, since the number of birds in the summer is influenced predominantly by the number of birds present the previous fall. Given the wide range of fall population numbers observed through the study period, the above-mentioned counties seem to exhibit survival rates that are independent of fall population size. Because overwinter survival does not seem to be influenced by population size or winter weather in these counties, factors influencing reproductive success are probably most crucial to these populations. Factors that have been shown to be influential to reproductive success include excessive hen mortality due to farming operations (Gates 1971), nest and hen predation (Dumke and Pils 1973), and variable springtime weather conditions (Besadny 1967, Stokes 1968).

Another pattern of survival was expressed in Millard and Sevier Counties. The fall and summer population indices were strongly correlated, as were the winter warmth and survival indices. This correlation implies density-independent overwinter survival as discussed for the counties previously mentioned, with winter temperatures also playing a part in population dynamics.

TABLE 1. A list of counties on which the analysis was run and weather stations used. All counties had 17 years of data except Beaver.

County	Weather station	Population data missing 1962-1979
Beaver	Beaver	1965
Box Elder	Brigham City	None
Cache	Logan	None
Duchesne	Roosevelt	None
Emery	Castle Dale	None
Juab	Nephi	None
Millard	Fillmore	None
Salt Lake	Salt Lake Airport	None
Sanpete	Moroni	None
Sevier	Richfield	None
Tooele	Tooele	None
Uintah	Vernal	None
Utah	Provo	None
Weber	Ogden	None

TABLE 2. Summary of the correlation analyses for each county. The table includes sample sizes used to determine fall and summer indices, correlation coefficients, and mean coefficients of determination (R^2) for groups of counties showing similar responses.

County	Hunters reporting fall harvest 95% C.I.	Km of summer pheasant routes 95% C.I.	Fall vs. summer index r =	Mean R ²	Winter warmth vs. survival index r =	Mean R ²
Beaver	34 ± 5.6	153 ± 47.2	0.67°°		0.15	
Box Elder	587 ± 65.2	248 ± 21.4	0.73°°		0.36	
Juab	79 ± 9.9	58 ± 8.2	0.80°°		0.20	
Salt Lake	548 ± 48.2	286 ± 86.8	0.70°°		-0.39	
Tooele	117 ± 17.4	103 ± 13.3	0.47°		0.25	
Utah	827 ± 77.0	569 ± 67.7	0.66°°	0.46	-0.04	0.07
Millard	220 ± 21.5	401 ± 42.9	0.67°°		0.57°°	
Sevier	185 ± 21.0	289 ± 37.1	0.66°°	0.44	0.62°°	0.35
Cache	437 ± 41.2	231 ± 58.0	0.39		0.61°°	
Sanpete	214 ± 25.7	262 ± 60.7	0.35	0.14	0.41°	0.27
Duchesne	148 ± 16.1	567 ± 28.5	-0.11		0.30	
Emery	135 ± 13.9	271 ± 46.4	0.18		0.34	
Uintah	141 ± 11.4	260 ± 42.7	-0.03	0.02	0.15	0.08
Weber	496 ± 47.8	149 ± 17.6	0.03	0.00	-0.49°	0.24

° = P < 0.05
°° = P < 0.01

Pheasants in the western plains have been shown to suffer direct storm-induced mortality during extremely harsh periods (Kimball et al. 1956, Lyon 1959). Pheasant losses in Millard and Sevier Counties may be a result of direct winter mortality, or mortality occurring during the nesting season due to winter weather, as suggested by Gates (1971). Analysis of winter mortality and vigor in these areas may help determine mechanisms of weather-induced mortality.

Significant correlations between the winter temperatures and the survival indices, with no statistically significant correlations between the fall and summer indices, were shown for Cache and Sanpete Counties. Winter temperature, although a significant factor to survival, accounted for only about 27 percent of the variability in the survival index. This fact, coupled with the lack of correlation between fall and summer indices, implies highly variable November to August survival rates for these counties, with winter temperatures playing a minor although important role.

Duchesne, Emery, and Uintah Counties showed no significant correlation in either of the correlation analyses. These results suggest

only that survival rates are highly variable and winter weather has very little influence on the pheasant populations. Any pheasant studies in these counties should look closely at the influences of population size, reproductive success, habitat, and food requirements on the ecology of these populations.

Weber County was unique in expressing a significant negative correlation between winter temperatures and the survival index with no relationship between fall and summer indices. In Weber County, survival rates seem to decrease when winter temperatures increase and are highly variable from year to year. These results are presented here with no attempt at interpretation.

Through a series of indices and their interactions, we have shown several patterns of overwintering population dynamics for pheasants in Utah. We are not suggesting that county boundaries delineate unique ecological situations. By using data from individual counties, we have been able to show that variation exists between different areas of the state. The methods outlined in this paper do not propose to give definitive solutions to particular population dynamics. They are intended to yield generalizations concerning

factors that may be influential on a particular population. These techniques can be used on any wildlife species for which there are population data as a preliminary analysis to provide guidance for major studies. Once crucial factors are identified, further research can be more precisely directed to determine specific factors that may be limiting survival.

ACKNOWLEDGMENTS

We thank S. D. Bunnell, J. T. Flinders, and K. T. Harper for their assistance during this project and also for critically reviewing the manuscript.

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DIETS OF SYMPATRIC RED FOXES AND COYOTES IN SOUTHEASTERN IDAHO¹

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ABSTRACT.— Scats of sympatric red foxes and coyotes from the upper Snake River Plain of southeastern Idaho were analyzed for composition. Rodent remains in general and those of cricetid mice in particular occurred more frequently in scats of red foxes during all seasons of the year than any other food items identified. Scats of coyotes differed significantly in content from scats of red foxes during winter and contained primarily pygmy rabbit remains. In summer, remains of pygmy rabbits, sheep, ground squirrels, yellow-bellied marmots, arthropods, and vegetation were found more frequently in scats of coyotes and remains of cricetid mice occurred more frequently in scats of red foxes. Red foxes and coyotes generally consumed similar food items but in different proportions. Based on the location of scats that were collected, red foxes and coyotes largely used different portions of the study area. Reasons for the preferential usage of habitat are discussed.

Although over 100 studies of food habits of red foxes (*Vulpes vulpes*) (Ables 1975) and numerous studies of diets of coyotes (*Canis latrans*) (Gier 1975) have been published, there is a lack of information on the food habits of these two canids in sympatry. Both species are versatile in their eating habits and readily consume animal and plant matter depending on season and availability. Both species readily feed on livestock and poultry when available and thus have come into conflict with human interests. Here we report the diets of red foxes and coyotes on the U.S. Sheep Experiment Station (USSES), where up to 10,000 sheep graze at various times of the year.

STUDY AREA AND METHODS

The USSES occupies approximately 11,000 ha of the upper Snake River Plain in Clark County, Idaho. The vegetation, described by Blaisdell (1958), is dominated by big sagebrush (*Artemisia tridentata*), with the primary understory species being thick spike wheatgrass (*Agropyron dasystachym*), bluegrass (*Poa* spp.), and mixed forbs. The area is grazed by sheep primarily in the spring and fall.

Scats from red foxes and coyotes were collected monthly from January 1976 to March

1978, primarily along dirt roads except when snow cover allowed cross-country snowmobile travel. Scat identification was made by observation of associated tracks, prey kills, and proximity to known dens and areas of preferred use. Scats were oven dried prior to storage and were later washed, separated, and prepared for analysis in a manner similar to that described by Johnson and Hansen (1979). The hair component of each scat was hand separated from the large (> 1mm) insoluble component.

Using a point frame method, 20 hair fragments from each scat were selected and identified by comparison to a reference collection of hair from prey species on the USSES. Hair was identified by medullary characters (Brunner and Coman 1974). Teeth were also used to verify the animal species consumed.

Relative abundance of small rodents on the USSES was estimated (Leslie 1952) with two parallel lines of 50 snap traps at 10 m intervals set for four consecutive nights. At least six sites per season were trapped during July 1976 and July 1977 in areas of varying sagebrush and bitterbrush cover. Fecal pellets of pygmy rabbits (*Brachylagus idahoensis*) were collected from seven permanent sites during 1977 and 1978 to monitor relative abundance of rabbits (Green and Flinders, 1980a). Rock chucks (*Marmota flaviventris*) and sage

¹This study was supported by USDA Western Regional Federal Cooperative Agreement 12-14-5001-264.

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grouse (*Centrocercus urophasianus*) were censused with spatial counts during summer 1976 and 1977.

A chi-square test was used to compare red fox and coyote diets and significance is reported at the 0.05 level.

RESULTS AND DISCUSSION

One hundred twenty-five scats from red foxes and 129 scats from coyotes were analyzed. They were grouped, according to date of collection, into one of two seasonal periods: winter (comprising inclusively the months September through February) and summer (comprising inclusively the months March through August). Small sample size precluded meaningful analyses of red fox and coyote scats between years. Therefore, the results reported reflect a biseasonal comparison of scat composition through a 27-month period (Table 1).

Sheep and yellow-bellied marmot remains occurred more frequently in red fox scats during the winter period, and Great Basin pocket mice (*Perognathus parvus*) occurred

more frequently in the summer period. Rodents in general and cricetid mice in particular (primarily *Peromyscus maniculatus*), occurred more frequently in scats of red foxes in both seasonal periods than any other food items identified.

Remains of pygmy rabbits were found most frequently in the scats of coyotes during the winter period and remains of Uinta ground squirrels (*Spermophilus armatus*), yellow-bellied marmots, arthropods, and vegetation were found more frequently in scats during the summer period. This was not unexpected, since yellow-bellied marmots and ground squirrels were in hibernation from approximately August until March and the likelihood of coyotes consuming arthropods and vegetation was higher in summer than in winter.

There were significant differences in the composition of scats of red foxes and coyotes during the winter and summer periods. During winter, pygmy rabbit remains were found more frequently in scats of coyotes, and remains of cricetid mice, birds, and vegetation were found more frequently in scats of red

TABLE 1. Bi-seasonal comparisons of contents of scats from sympatric red foxes and coyotes in southeastern Idaho.

	Winter (September–February)				Summer (March–August)			
	Red fox (n = 38)		Coyote (n = 64)		Red fox (n = 87)		Coyote (n = 65)	
	% occur. ¹	% vol.	% occur.	% vol.	% occur.	% vol.	% occur.	% vol.
Rabbits (total)	(32)	(22)	(67)	(70)	(32)	(14)	(38)	(22)
Pygmy rabbit (<i>Brachylagus idahoensis</i>)	29	22	64	69	22		38	22
Jackrabbit (<i>Lepus townsendii</i>)	3	t	3	1				
Rodents (total)	(71)	(51)	(39)	(16)	(82)	(69)	(74)	(65)
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	5						31	
Uinta ground squirrel (<i>Spermophilus armatus</i>)			2		1		17	
Great Basin pocket mouse (<i>Perognathus parvus</i>)	3		3		17		12	
Cricetid mice ²	68		39		75		43	
Other rodents	5		6		16	5		
Domestic sheep	34	23	25	13	17	14	32	12
Birds	13	t	3	t	10	t	12	t
Arthropods	18	t	6	t	21	t	49	t
Plant matter ³	34		17		34		66	

¹Percent of scats that contained particular food items.
²Primarily *Peromyscus maniculatus*.
³Volume of plant matter was not estimated.

foxes. In the summer period, remains of pygmy rabbits, sheep, ground squirrels, yellow-bellied marmots, arthropods, and vegetation were found more frequently in scats of coyotes, and remains of cricetid mice occurred more frequently in scats of red foxes.

An index of similarity (SI) was calculated for scat composition of red foxes and coyotes for the winter and summer periods using the formula $SI = (\Sigma \text{ minimum value} \div \Sigma \text{ maximum value}) (100)$. The SI for composition of scats of red foxes and coyotes during the winter period was 48.5 percent and during the summer period was 44.5 percent. An SI of 100 percent would exist when scats were identical in composition.

The density of small mammals was estimated to be 44/ha in the summer 1976 and 74/ha in the summer 1977. Deer mice were the predominant rodent during both years (59 and 90 percent, respectively). The density of yellow-bellied marmots and sage grouse were 0.075 and 0.475/ha, respectively, in 1976 and 0.57 and 0.97/ha, respectively, in 1977. Fecal pellet counts of pygmy rabbits were not significantly different during the two years of the study.

Sheep remains were found in scats of red foxes and coyotes throughout the year. In winter, the sheep remains were obtained as carrion because the sheep were kept in pens where they were not vulnerable to predation. Sheep carcasses were not removed from the range, and in winter they may have provided an important source of food for both canids. One of us (Green) observed sheep carcasses uncovered from beneath several feet of snow by red foxes and coyotes. They were frequently fed upon by both predators. During the spring, lamb remains were observed at the entrance to several fox dens. Lambs die of exposure and/or disease in the spring and may be consumed by both red foxes and coyotes. Both predators may also kill and consume sheep.

Several studies have shown that, in certain areas, coyotes relied heavily upon rabbits (*Sylvilagus* spp.) and/or hares (*Lepus* spp.) (Bond 1937, Sperry 1941, Korschgen 1957, Clark 1972). In this study area, pygmy rabbits provided a major portion of the diet of coyotes. Scats from coyotes collected during January and February were often composed

entirely of remains from pygmy rabbits. During the period of this study, cottontail rabbits (*S. nuttallii*) and white-tailed jackrabbits (*L. townsendii*) were rarely observed. Although relatively small, pygmy rabbits were the largest prey species available on the USSES during the latter half of the winter period. [Adult pygmy rabbits weigh approximately 450 g (Green and Flinders 1980b); adult Nuttall's cottontail rabbits weigh approximately 800 g (Orr 1940); white-tailed jackrabbits weigh approximately 2.7 kg (Flinders and Hansen 1972).]

Scats from coyotes were collected throughout the 11,000 ha of the USSES although more (73 percent) were found in the northern half. Scats from red foxes were also found throughout the study area, but a majority (80 percent) was collected in the southern half. In addition, red foxes were rarely observed anywhere but in the southern portion of the USSES. The entire study area is sagebrush-grass type with no readily apparent differences in habitat between the northern and southern portions. Rodent trapping and other censusing of wildlife indicated that items of prey were generally found in similar concentrations in all areas sampled.

We propose that both canids in this study, and particularly red foxes, showed a preferential usage of habitat for the following reasons. For over 60 years the plan of sheep management at the USSES has been to graze the southern portion of the range with ewes and their new lambs beginning approximately May 1. The death of lambs from disease and starvation is often augmented by adverse weather conditions, thus providing carrion for carnivores. The availability of carrion corresponds closely to the time of whelping, raising, and rearing of red fox pups. Since adult red foxes are likely to remain in the same area for life (Ables 1975), it is conceivable that generations of red foxes have keyed on this area for food; both carrion and vulnerable prey (lambs). At least five active den sites of red foxes were located in the southern portion of the USSES during this study. Red foxes have not been actively hunted in this area.

Several factors have increased human killing of coyotes since the early 1970s. Fur prices escalated, causing increased sport

hunting, trapping, snowmobile chasing, and aerial gunning of coyotes. The latter two methods are extremely effective in eliminating coyotes in sagebrush-grass habitat. The use of poisons for coyote control was prohibited, perhaps intensifying the effort, particularly in sheep-producing areas, to remove coyotes at every opportunity.

Since the USSES headquarters is located in the southern portion of the range, human activity (moving sheep to and from headquarters for lambing and shearing, hauling water, and inhabiting sheep wagons) is more intense than in the northern area. Human pressure on coyotes, the concurrent relative disregard for red foxes, and the opportune pup-rearing circumstances for red foxes in the southern portion of the range may all have contributed to the differential use of habitat by red foxes and coyotes observed in this study.

Although little is known of the inter-specific relationships of red foxes and coyotes, there is some indication that red foxes may readily occupy a suitable niche vacated by coyotes as a result of predator control or other reasons (Gier 1975, U.S. Fish and Wildlife Service 1978). It is not known how long red foxes and coyotes have occupied this study area, but, because both these predators often utilize similar food items and occupy similar habitat, it is doubtful that their relationship is static.

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THE EFFECT OF ELEVATED TEMPERATURE ON COPPER TOXICITY TO THE THERMOPHILIC ALGA *SYNECHOCOCCUS LIVIDUS* (CYANOPHYCEAE)

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ABSTRACT.— The hypothesis that temperature influences the toxicity of copper to thermophilic Cyanophyceae was tested in a laboratory study with *Synechococcus lividus*. This thermophile was tested at copper concentrations from 0 to 200 $\mu\text{g/l}$, and temperatures from 40.0 to 50.0 C. It was found that an interaction between increased copper and temperature significantly decreased the rate of carbon assimilation, chlorophyll content, and photosynthetic efficiency.

Geothermal springs represent a remarkably unique and stable environment with respect to a large number of physical and chemical parameters. The temperatures of these springs rarely vary more than 2 C throughout the seasons. A constant flow rate with laminar flow characteristics exists which, among other things, minimizes the forces of erosion. Light intensity is high. The area around hot springs is usually devoid of trees and the water column is shallow. Nutrient replenishment is continuous in the flowing water system, so that nutrient deficiencies probably do not develop (Brock 1970).

Even in these seemingly ideal conditions, only a restricted flora exists. Due to the elevated temperatures of the thermal spring environment—approximately 50 C to well above the boiling point in fumaroles—prokaryotes are usually the sole inhabitants (Brock 1967a). The Cyanophyceae present have an upper temperature limit of 73–75 C. These algae are not merely subsisting, but are actually growing and thriving at a given location (Brock 1967b). This heat tolerance seems to be due to a number of factors, including the thermal stability of their photosynthetic membrane systems, the low Q_{10} value of respiratory rates preventing acceleration to lethal catabolism, the heat stability of the algal protoplasmic structures and the capacity of their proteins to endure high temperatures without denaturation, and the lack of competition in the environment

(Brock 1974, Lewin 1962). Luxuriant growth is to be expected in these locations.

However, visible degradation of the algal mats has occurred in many thermal springs of Yellowstone National Park. This deterioration is particularly noticeable in those areas which are heavily frequented by visitors.

Changes in water temperature, nutrient concentration, flow rate, etc., may be eliminated as possible mechanisms for degradation due to the stability of the environment. An external factor exists as the remaining possibility—i.e., the introduction of copper coinage to the thermal springs (R. A. Hutchinson, Yellowstone National Park Geologist, pers. comm.).

Copper has long been widely used as an algicide. The recommended dose for algal control in alkaline water ranges from 0.2 to 2.0 mg/l (Trainor 1978), but can be as low as 50 $\mu\text{g/l}$ for *Chlorella* (Bartlett et al. 1974). The chemical analysis of some of the major thermal springs of Yellowstone National Park indicates the copper concentration ranges from 1 to 9 $\mu\text{g/l}$ (Brock, 1978), which appears to be much too low for the demonstrated algicidal effects. However, this does not preclude the possibility of increased toxicity at the elevated temperatures found in the thermal springs. These temperatures approach the critical maximum for life itself.

The possibility, therefore, exists that even low copper concentration in a thermal environment produce a detrimental effect on

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algal mats—i.e., an interactive effect exists between copper and heat.

METHODS

Axenic cultures of *Synecococcus lividus* (R. Castenholz, Department of Biology, University of Oregon, pers. comm.) were maintained in a general growth medium (Miller et al. 1978) with a 12-hour light:dark cycle. Cultures were frequently diluted to maintain cells in exponential growth phase.

Batch cultures were acclimated to a temperature (± 0.01 C) for one week prior to each experiment. Following this acclimation period the culture volume was subdivided, and to each aliquot an amount of copper was added as $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$. Final concentrations

were 0, 50, 100, 150, and 200 $\mu\text{g Cu/l}$. Aliquots were then incubated a further 24 hours after which each treatment was dispensed into triplicate 125 ml glass bottles for measurement of carbon assimilation, and an amount was filtered for chlorophyll analysis.

To each of the replicate bottles, we added 5 μCi of ^{14}C bicarbonate (New England Nuclear). Cells were incubated for three hours, then membrane filtered and washed with distilled water. Filters were dried, placed in omnifluor, and activity measured by liquid scintillation. Because each treatment was handled in the same manner, radioactive counts per minute (CPM) were directly comparable among treatments. Chlorophyll-a was estimated from the optical density of ethanol extracts.

TABLE 1. Relative carbon assimilation (counts per minute) at experimental temperatures and copper concentrations.

Degrees C	$\mu\text{g/l Cu}$				
	0	50	100	150	200
40.0	31409	8339	8595	7505	2922
	47990	10980	8027	4508	1259
	49364	9436	7765	4059	1032
	46400	11315	11415	3382	2662
	44649	10932	9174	2421	1284
	44459	9157	11700	4087	1221
42.5	28340	26293	9845	2294	1076
	31502	16756	8746	2468	631
	39546	21045	7263	1845	463
	45936	13467	8034	2932	1399
	51584	12640	6336	1317	2477
	46953	12162	7490	3420	352
45.0	218047	131760	53929	26266	8420
	195315	138318	53482	24028	6977
	165850	126580	46425	24480	4832
	184091	113685	39251	23552	2999
	178200	131783	29053	21473	2426
	147796	137110	38914	20091	1499
47.5	126228	46272	16153	4162	1033
	140663	29294	13862	2798	903
	155604	26466	10830	2287	1459
	164761	22688	11420	1932	619
	155644	26186	11849	1257	580
	147319	22365	10548	2040	520
50.0	53933	37702	11616	4812	521
	54506	33803	11605	6573	1762
	62672	24093	12541	1846	803
	73887	21548	9130	1942	4422
	79563	17767	7518	2232	506
	62200	17893	12252	4387	826

This procedure was repeated at each of five growth temperatures: 40.0, 42.5, 45.0, 47.5, and 50.0 C. To facilitate statistical manipulation, all CPM and chlorophyll data were normalized with respect to the control treatment (0 $\mu\text{g/l}$ Cu) to eliminate differences among treatments due to variations in starting population density.

RESULTS AND DISCUSSION

Carbon assimilation data in terms of CPM are shown in Table 1. At all experimental temperatures increased copper concentration led to decreased carbon assimilation so that, at 200 μg , Cu/l assimilation was less than 5 percent of the control value. Using analysis of variance for two-way classification (Mendenhall et al. 1977) we found a significant interaction ($F_{16,125} = 3.31$, $p < 0.01$) between temperature and copper concentration.

Two possible causes for decreased carbon assimilation include decreased chlorophyll content per cell and depressed photosynthetic efficiency measured as carbon assimilation per unit chlorophyll. Table 2 shows

the chlorophyll concentration of aliquot cultures after only 24 hours of incubation in the presence of copper. Again, at all experimental temperatures there is a significant decrease in chlorophyll with increased copper. There was also significant interaction ($F_{16,25} = 8.56$, $p < 0.01$) between temperature and copper.

Photosynthetic efficiency as measured by carbon assimilation per unit chlorophyll similarly decreased with increasing copper concentration (Table 3). Further, there was a significant interaction ($F_{16,125} = 12.44$, $p < 0.01$) between temperature and copper.

From these data it appears that copper interacting with temperature can cause significant depression of the photosynthetic activity of *Synechococcus lividus*. This appears to be caused by a decrease in chlorophyll content of the cell, and a lowered photosynthetic efficiency. It is possible that at temperatures higher than those examined only minute concentrations of copper may prove to be toxic to *S. lividus*. If this is so, and if our results may be extended to other thermophilic cyanophytes, this is a possible mechanism to

TABLE 2. Chlorophyll-a concentrations ($\mu\text{g/l}$) of aliquot cultures following 24-hour incubation with various copper concentrations.

Degrees C	$\mu\text{g/l}$ Cu				
	0	50	100	150	200
40.0	52	42	41	37	31
	49	40	37	36	29
42.5	50	38	27	31	28
	47	36	34	31	28
45.0	98	80	64	75	58
	98	69	64	77	61
47.5	87	63	59	42	34
	90	62	66	41	33
50.0	85	55	48	37	27
	83	58	51	38	26

TABLE 3. Relative photosynthetic efficiency as CPM ^{14}C assimilated per mg chlorophyll. Control treatments were normalized to 100 percent.

Degrees C	$\mu\text{g/l}$ Cu				
	0	50	100	150	200
40.0	100	28	28	14	6
42.5	100	55	31	9	5
45.0	100	94	37	16	4
47.5	100	27	12	3	2
50.0	100	59	28	12	7

explain the current deterioration of algal mats in many thermal springs.

ACKNOWLEDGMENTS

We thank Dr. R. Castenholtz, who provided cultures of *S. lividus*, and the National Park Service for permission to collect water samples in Yellowstone National Park for copper analysis.

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AVIFAUNA OF THE MT. DELLENBAUGH REGION, SHIVWITS PLATEAU, ARIZONA¹

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ABSTRACT.— An investigation of the avifauna of Mt. Dellenbaugh, Arizona, and nearby areas on the Shivwits Plateau was conducted during fall 1974 and during spring and summer 1975. A total of 92 species of birds was recorded, of which 56 were considered resident. Species composition is discussed in relation to habitat.

From an ornithological standpoint, the Shivwits Plateau in northwestern Arizona has been neglected. In fact, bird studies in the entire region (northwestern Arizona, southwestern Utah, and adjoining parts of southeastern Nevada) have been limited. The need for work in this part of Arizona is evident from an examination of distribution maps in *Birds of Arizona* (Phillips et al. 1964) and is further emphasized by Monson and Phillips (1964:178). Despite this lack of information, virtually no work has been conducted on the Shivwits Plateau and nearby areas.

Mt. Trumbull, located approximately 50 km NE of Mt. Dellenbaugh on the Uinkaret Plateau, was visited by Huey (1939) for approximately two weeks in late July; Mt. Trumbull is the closest reported study area to that part of the Shivwits Plateau covered by the present report. Farther east, Rasmussen (1941) and Jenks (1931) have reported on bird communities of the Kaibab Plateau. Investigations on avifauna of south central and southwestern Utah have been somewhat more extensive (Presnall 1935, Hardy and Wiggins 1940, Behle 1943, Behle et al. 1958, Wauer and Carter 1965) but have not included the Shivwits Plateau region. Farther west, several authors have examined the desert avifauna of the Virgin River Valley in Nevada, Arizona, and Utah (Tanner 1927, Wauer and Russell 1967, Wauer 1969, Behle 1976, Whitmore 1977).

In 1975, a study was initiated by the U.S. National Park Service Cooperative Resources Studies Unit located at the University of Nevada, Las Vegas, to document distribution of plants and animals within the Lake Mead

National Recreation Area. The northern boundary of the recreation area crosses the southern edge of the Shivwits Plateau, close to Mt. Dellenbaugh. As a consequence, several trips were made to the Shivwits Plateau by members of the NPS study team, with observations taken on occurrence and distribution of flora and fauna. The present paper presents an account of bird species observed. Distribution of birds within different habitats is discussed.

Place names and topographical information used in the present report are taken from U.S.G.S. 1:250,000 topographical maps.

STUDY AREA

The Shivwits Plateau is primarily flat tableland, with occasional lava-capped buttes and isolated mountains. Over much of the southern part of the plateau elevation is approximately 1830 m. Northward, the plateau stretches toward Utah, gradually decreasing in elevation. The southern boundary is marked by an abrupt descent to the Sanup Plateau, at 1370 m. Numerous steep-walled canyons dissect the plateau, leading eventually to the Colorado River. Mt. Dellenbaugh, the highest peak in the southern part of the plateau, reaches an elevation of 2130 m. Approximately 8 km NE is Yellow John Mountain, which reaches an elevation of 2060 m (Fig. 1).

Observations are primarily from the vicinity of Mt. Dellenbaugh and Green Springs Canyon; additional observations were made on a trip along Twin Point (Fig. 1). Various distinct habitats occur at different locations

¹This work was supported by NPS/UNLV Contracts 8000-4-0031/CX 8000-6-0034.

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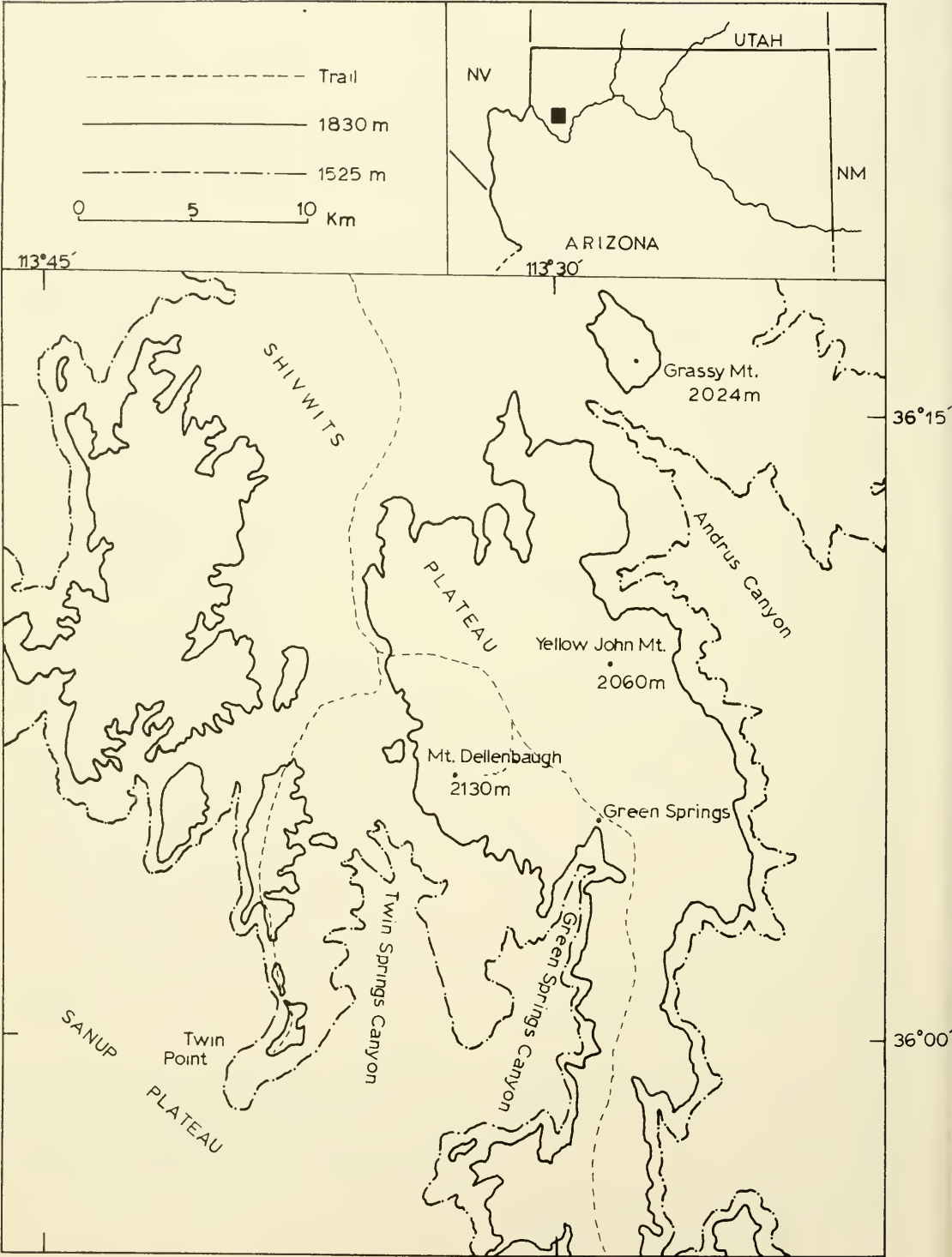


Fig. 1. The southern part of the Shivwits Plateau is shown, with sites mentioned in the report indicated. Location of the plateau within Arizona is shown in the upper right.

and are briefly described below. Plant identification was by members of the NPS study team.

Predominant vegetation over most of the Shivwits Plateau is pinyon pine (*Pinus monophylla*) – juniper (*Juniperus osteosperma*) woodland. Understory is sparse within this open, relatively xeric woodland, consisting primarily of sagebrush (*Artemisia*) and scrub oak (*Quercus*). Locally concentrated patches of oaks and sagebrush produce a more brushy appearance in certain areas (e.g., southern end of Twin Point).

Ponderosa pine (*Pinus ponderosa*) occurs in limited amounts, principally along drainages where soils are deeper and moisture conditions higher. Scattered individuals occur throughout the area. Due to drainage patterns, ponderosas occur primarily as belts interspersed in pinyon-juniper woodland and bordering open sagebrush fields. Understory and ground cover are sparse, with a mixed shrub assemblage that includes species of oak, sagebrush, mountain mahogany (*Cercocarpus montanus*), and others.

Upper slopes of Mt. Dellenbaugh and edges and slopes of various canyons are covered with a mixed assemblage of relatively brushy shrubs and trees, which produces a chaparral type habitat. Although oaks, including scrub oak (*Quercus turbinella*), Gambel oak (*Q. gambelii*), and wavyleaf oak (*Q. undulata*), are particularly abundant, numerous other shrubs also occur, including mountain mahogany and manzanita (*Arctostaphylos pungens*). Particularly on the slopes of Mt. Dellenbaugh, New Mexican locust (*Robinia neomexicana*) occurs in locally dense stands.

Large expanses of sagebrush (*Artemisia tridentata*) occur at a number of locations on the plateau. In a number of instances, juniper trees have been cleared, and large piles of dead trees add a significant component to the habitat. Additional plant species occurring with sagebrush include rabbit brush (*Chrysothamnus* spp.), snake weed (*Gutierrezia microcephala*), and others.

Several ranchers graze cattle on the plateau, and a number of ponds have been constructed to supply water. Vegetation is virtually absent around some ponds, but

others are bordered by relatively dense stands of shrubs, particularly rabbit brush.

All habitat types described above occur at or near Mt. Dellenbaugh. A large sagebrush field occurs just north of the mountain and has been maintained in part for use as a landing strip. Cattle also graze over parts of the field; several ponds occur in or around the perimeter of the field. Pinyon-juniper woodland surrounds much of the mountain and extends south to the plateau edge. Pinyon-juniper extends part way up the slopes of the mountain, particularly on the northern face. Ponderosa pine occurs in belts near the base of the mountain, bordering the sagebrush at numerous points. Mixed oak scrub predominates over much of the mountain slope.

Green Springs Canyon is located approximately 6 km ESE of Mt. Dellenbaugh (Fig. 1). Pinyon-juniper woodland predominates over much of the surrounding plateau. An open ponderosa pine stand occurs at the head of the canyon. The stand was logged at some time in the past, and presently is composed of large, widely spaced trees, forming a more parklike appearance than is found elsewhere. Patches of sagebrush occur at scattered locations, but large expanses are absent from the area. Canyon slopes and edges are covered by oak scrub, with Gambel oak particularly prevalent in patches on midslopes. The canyon bottom is quite moist and supports a limited amount of riparian vegetation.

Twin Point is predominantly pinyon-juniper woodland with oak scrub along the plateau rim and at the southern end of the point. Large sagebrush fields occur at several locations along the plateau.

METHODS

Mt. Dellenbaugh was visited in fall 1974 (28 September, 4–5, 12–14 October), and spring (17–18 May) and summer (7,9,27–29 June) 1975. Green Springs Canyon was visited 28–29 September 1974 and 16 May and 6,8 June 1975. A trip was made to the southern end of Twin Point 6–7 October 1974; the northern end was briefly visited again on 7 June 1975. Thus, a total of 19 days was spent in field observations.

No regular censuses were conducted during the study, but all habitats were surveyed

on a regular basis. Observations were conducted on foot and were concentrated in the morning, from approximately one-half hour prior to sunrise until approximately 4–5 hours after sunrise. Additional observations were made throughout the day with a second concentrated effort in the evening. During observation periods, a count was kept of the number of individuals of each species seen. The trip out from Twin Point involved periodic stops for observation as well as observations from the vehicle.

Several additional trips were made to the Mt. Dellenbaugh area in spring and summer 1976 by other members of the study team. Observed species new to the area are listed at the end of the Appendix.

Species were classified as resident (including those thought to be permanently resident on the plateau and those that breed in the area but depart for winter), migrant (those passing through the area in fall and/or spring as part of a regular migration), and visitors (including those that breed elsewhere, frequently at lower elevations, which appear on the Shivwits Plateau irregularly but not during normal migration periods). Most visitors were observed only once.

Relative abundance designations were determined from the number of days on which the species was observed, together with the number of individuals observed. Abundant species were designated as those seen on approximately 80 percent or more of trips, common species were observed 60–80 percent of the time, uncommon species were observed 40–60 percent of the time, and rare species were observed less than 40 percent of the time. The number of individuals observed was used to modify these categories. Thus, a species seen on all trips, but with only 1–2 individuals recorded each time was designated common. Alternatively, species seen on few

trips, but seen in large numbers on each trips, were designated as common. This method is subjective, but with criteria consistently applied does provide an index of abundance.

RESULTS

A total of 92 species was recorded during visits to the Shivwits Plateau (Appendix). Of these, 13 were observed only in 1976, including one summer resident (Poor-will), 3 migrants, and 9 visitors. The failure to record additional summer residents suggests that coverage in 1975 was relatively complete. The following discussions that involve habitat preference will not include these species, due to a lack of personal observations.

Of the total observed, 56 species were considered probable breeding residents, 24 were migrants, and 12 were visitors. More species were observed in pinyon-juniper woodland than in other habitats (Table 1), although the numbers in oak scrub and ponderosa pine were comparable. Among residents, a greater number were recorded from oak scrub habitat (35) than from pinyon-juniper (34) or ponderosa pine (31). Migrants were considerably more common in pinyon-juniper and ponderosa pine stands than in oak scrub. The number of resident species observed on fields or at ponds were similar (Table 1). Heavy use of ponds by migrants (29 percent of the total observed at ponds) resulted in a higher species total from ponds than from fields.

Thirty-two species were observed in only one habitat (Table 2). Of these, 15 were resident, 14 were migrant, and 3 were visitors. Only a single resident species (Black-throated Gray Warbler) was restricted to pinyon-juniper woodland, although this habitat is predominant over the plateau. More species, 5, were restricted to oak scrub habitat than to any other habitat. More than twice as

TABLE 1. Distribution within habitats is shown for species recorded at or near Mt. Dellenbaugh, Arizona, 1974–1975.

	Pinyon-juniper	Ponderosa pine	Oak scrub	Sagebrush fields	Ponds
Residents	34	31	35	18	18
Migrants	11	7	7	3	8
Visitors	0	1	0	0	2
Total	45	39	42	21	28

many migrants were observed only at ponds (7) than in any other habitat (3 in pinyon-juniper). In contrast to residents, only one migrant was restricted to oak scrub areas. Visitors also were slightly more frequent at ponds than in other habitats.

DISCUSSION

Close proximity of several distinct habitat types may influence the species composition of an area. Habitat variability is greater at Mt. Dellenbaugh than at Green Springs Canyon, and a greater number of species were resident at Mt. Dellenbaugh (51) than at the latter area (33). Four species, including 3 owls, were recorded only from Green Springs Canyon. In addition, Canyon Wrens were present along the canyon slopes at Green Springs. Presence of large sagebrush fields and several cattle ponds accounted for 4 of 15 species recorded only from Mt. Dellenbaugh (Killdeer, Common Nighthawk, Horned Lark, Mountain Bluebird); Turkey Vultures and Red-tailed Hawks also were seen more frequently over fields or at ponds.

Species composition at Mt. Dellenbaugh and surrounding areas was similar to that reported by Huey (1939) for Mt. Trumbull. Of 51 species included by Huey in his report, 43 were from the Mt. Trumbull region, with 8 from areas farther north. Of the 43, 38 were considered resident at Mt. Trumbull, with 3 more possibly resident in the area. Of the 43 birds seen at Mt. Trumbull, 32 were considered resident at Mt. Dellenbaugh, 5 were not considered resident, and 6 were not observed at Mt. Dellenbaugh. Seven of the 8 species recorded by Huey (1939) from areas north of Mt. Trumbull were seen at Mt. Dellenbaugh; 4 were considered resident. The present report covers a greater area than did Huey (1939), which accounts in part for the higher

resident species total from Mt. Dellenbaugh (56 species). In addition, Mt. Trumbull reaches a higher elevation (2447 m) than Mt. Dellenbaugh, accounting in part for some of the species differences between the two areas.

The present report presents a preliminary species list, but considerable additional work in the area is needed. Bird communities on the more isolated Sanup Plateau have, for example, not been investigated at all. Additionally, although pinyon-juniper woodland forms a fairly continuous cover over the plateau, additional habitat types are present as more or less isolated patches of varying size. An examination of bird use of these habitat patches, with respect to area and degree of isolation, would prove interesting.

ACKNOWLEDGMENTS

I would like to thank G. T. Austin for additional bird records and J. Holland for plant identifications.

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TABLE 2. Distribution of species restricted to one habitat. Species were observed at or near Mt. Dellenbaugh, Arizona, 1974-1975.

	Pinyon-juniper	Ponderosa pine	Oak scrub	Sagebrush fields	Ponds
Residents	1	4	5	2	3
Migrants	3	2	1	1	7
Visitors	0	1	0	0	2
Total	4	7	6	3	12

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APPENDIX

Species observed on Shivwits Plateau, Arizona. Observations were made at Mt. Delenbaugh (MD), Green Springs Canyon (GS), and Twin Point (TP). Residential status (R) is noted (M = migrant, V = visitor, PR and SR = permanent and summer residents, respectively). Relative abundances are indicated by season (F = fall, SP = spring, SU = summer). Five habitats are distinguished (PJ = pinyon-juniper woodland, PP = ponderosa pine, OS / oak scrub, F = sagebrush fields, P = ponds). Nomenclature follows AOU Check-list of North American Birds, 1957 ed., with 32nd and 33rd supplements.

Species	Abundance				Location			Habitat				
	R	F	SP	SU	MD	GS	TP	PJ	PP	OS	F	P
Green-winged Teal <i>Anas crecca</i>	M	X					+					+
Ruddy Duck <i>Oxyura jamaicensis</i>	M		X		+							+
Turkey Vulture <i>Cathartes aura</i>	SR		U	C	+					+	+	+
Sharp-shinned Hawk <i>Accipiter striatus</i>	SR	U	U		+	+		+	+	+		
Cooper's Hawk <i>Accipiter cooperi</i>	M	U			+		+	+	+	+		+
Red-tailed Hawk <i>Buteo jamaicensis</i>	PR	U	R	U	+					+	+	
Golden Eagle <i>Aquila chrysaetos</i>	PR	X					+				+	
American Kestrel <i>Falco sparverius</i>	SR	U	U	C	+	+	+	+		+	+	+
Killdeer <i>Charadrius vociferus</i>	SR		C	C	+							+
Spotted Sandpiper <i>Actitis macularia</i>	M		X		+							+
Long-billed Dowitcher <i>Limnodromus scolopaceus</i>	M		X		+							+
Black-necked Stilt <i>Himantopus mexicanus</i>	M		X		+							+
Bonaparte's Gull <i>Larus philadelphia</i>	M		X		+							+
Band-tailed Pigeon <i>Columba fasciata</i>	SR	C		C	+	+		+	+	+		

Appendix continued.

Species	R	Abundance			Location			Habitat				
		F	SP	SU	MD	GS	TP	PJ	PP	OS	F	P
Mourning Dove <i>Zenaida macroura</i>	SR	R	A	A	+	+	+	+	+	+	+	+
Screech Owl <i>Otus asio</i>	PR			X		+		+		+		
Flamulated Owl <i>Otus flameolus</i>	SR		X			+		+		+		
Great Horned Owl <i>Bubo virginianus</i>	PR		X			+		+	+			
Common Nighthawk <i>Chordeiles minor</i>	SR			C	+						+	
White-throated Swift <i>Aeronautes saxatalis</i>	SR	C	C	A	+	+	+			+		+
Broad-tailed Hummingbird <i>Selasphorus platycercus</i>	SR		U	C	+	+		+	+	+		
Common Flicker <i>Colaptes auratus</i>	SR	A	A	A	+	+	+	+	+	+		+
Williamson's Sapsucker <i>Sphyrapicus thyroideus</i>	M	X				+			+			
Hairy Woodpecker <i>Dendrocopos villosus</i>	PR	C	C	C	+	+	+	+	+	+		
Cassin's Kingbird <i>Tyrannus vociferans</i>	SR		A	A	+	+	+	+	+	+	+	+
Ash-throated Flycatcher <i>Myiarchus cinerascens</i>	M		U		+			+		+		
Black Phoebe <i>Sayornis nigricans</i>	V			X	+				+			
Say's Phoebe <i>Sayornis saya</i>	V			X	+							+
Gray Flycatcher <i>Empidonax wrightii</i>	SR		U	C	+	+		+	+	+		
Western Wood Pewee <i>Contopus sordidulus</i>	SR	R		C	+	+		+	+	+		
Horned Lark <i>Eremophila alpestris</i>	SR			R	+							+
Violet-green Swallow <i>Tachycineta thalassina</i>	SR		A	A	+	+	+		+	+	+	+
Rough-winged Swallow <i>Stelgidopteryx ruficollis</i>	V			X			+					+
Steller's Jay <i>Cyanocitta stelleri</i>	PR	U	U	U	+	+		+	+	+		
Scrub Jay <i>Apelocoma coerulescens</i>	PR	A	U	C	+	+	+	+		+	+	
Common Raven <i>Corvus corax</i>	PR	A	U	C	+	+	+	+	+	+	+	+

Appendix continued.

Species	R	Abundance			Location			Habitat				
		F	SP	SU	MD	GS	TP	PJ	PP	OS	F	P
Pinyon Jay <i>Gymnorhinus cyanocephalus</i>	PR	A	U	C	+			+	+	+		+
Mountain Chickadee <i>Parus gambeli</i>	PR	C	C	A	+	+		+	+	+		
Plain Titmouse <i>Parus inornatus</i>	PR	A	C	A	+	+	+	+	+	+		
Common Bushtit <i>Psaltiriparus minimus</i>	PR	A	U		+		+	+		+		
White-breasted Nuthatch <i>Sitta carolinensis</i>	PR	C	U	C	+	+		+	+			
Pygmy Nuthatch <i>Sitta pygmaea</i>	PR	A	U	A	+	+			+			
Brown Creeper <i>Certhia familiaris</i>	PR	C		R	+	+			+			
House Wren <i>Troglodytes aedon</i>	SR			R	+					+		
Bewick's Wren <i>Thryomanes bewickii</i>	SR	C		U	+	+	+	+		+	+	
Canyon Wren <i>Catherpes mexicanus</i>	SR	U		R		+	+			+		
Rock Wren <i>Salpinctes obsoletus</i>	SR	C	R	U	+	+	+	+		+	+	
Mockingbird <i>Mimus polyglottos</i>	SR			U	+			+				+
Sage Thrasher <i>Oreoscoptes montanus</i>	M	X					+	+				
American Robin <i>Turdus migratorius</i>	SR	R	R	C	+	+	+	+	+	+		+
Western Bluebird <i>Sialia mexicana</i>	SR	C	C	C	+	+	+	+	+		+	
Mountain Bluebird <i>Sialia currocoides</i>	SR	A	C	C	+						+	+
Townsend's Solitaire <i>Myadestes townsendi</i>	M	C			+	+	+	+		+		
Blue-gray Gnatcatcher <i>Poliophtila caerulea</i>	SR			C	+	+				+		
Ruby-crowned Kinglet <i>Regulus calendula</i>	M	C			+	+	+	+	+			
Gray Vireo <i>Vireo vicinior</i>	M	R	R		+				+	+		
Solitary Vireo <i>Vireo solitarius</i>	SR			C	+	+		+	+			
Warbling Vireo <i>Vireo gilvus</i>	M		X		+			+				
Virginia's Warbler <i>Vermivora virginiae</i>	SR		U	C	+	+				+		

Appendix continued.

Species	R	Abundance			Location			Habitat				
		F	SP	SU	MD	GS	TP	PJ	PP	OS	F	P
Yellow-rumped Warbler <i>Dendroica coronata</i>	M	A	A		+	+	+	+		+	+	
Black-throated Gray Warbler <i>Dendroica nigrescens</i>	SR		A	A	+			+				
Grace's Warbler <i>Dendroica graciae</i>	SR		A	A	+	+			+			
Wilson's Warbler <i>Wilsonia pusilla</i>	M	U			+		+	+	+			
Brewer's Blackbird <i>Euphagus cyanocephalus</i>	M	R	R		+		+					+
Brown-headed Cowbird <i>Molothrus ater</i>	SR		A	C	+		+	+	+			+
Hepatic Tanager <i>Piranga flava</i>	SR			C	+	+			+			
Black-headed Grosbeak <i>Pheucticus melanocephalus</i>	SR		U	C	+	+		+	+	+		
Cassin's Finch <i>Carpodacus cassinii</i>	M	U			+	+		+	+			
House Finch <i>Carpodacus mexicanus</i>	SR	U		C	+	+	+	+	+	+		+
Lesser Goldfinch <i>Carduelis psaltria</i>	SR			C	+				+			
Green-tailed Towhee <i>Pipilo chlorura</i>	M		X		+				+			
Rufous-sided Towhee <i>Pipilo erythrophthalmus</i>	SR	C	C	A	+	+	+	+		+	+	
Savannah Sparrow <i>Passerculus sandwichensis</i>	M	X			+						+	
Lark Sparrow <i>Chondestes grammacus</i>	SR	U	A	C	+	+		+	+		+	+
Dark-eyed Junco <i>Junco hyemalis</i>	PR	A	U	R	+			+	+		+	
Chipping Sparrow <i>Spizella passerina</i>	SR	C	C	A	+	+		+	+	+	+	
Brewer's Sparrow <i>Spizella breweri</i>	SR			U			+					+
Black-chinned Sparrow <i>Spizella atrogularis</i>	SR		U	U	+	+				+		
White-crowned Sparrow <i>Zonotrichia leucophrys</i>	M	A			+	+	+	+	+	+	+	
Species observed only in 1976.												
Poor-will <i>Phalaenoptilus nuttallii</i>	SR				+							
Acorn Woodpecker <i>Melanerpes formicivorus</i>	V				+							

Species	R	Abundance			Location			Habitat				
		F	SP	SU	MD	GS	TP	PJ	PP	OS	F	P
Western Kingbird <i>Tyrannus verticalis</i>	V				+							
Dusky Flycatcher <i>Empidonax oberholseri</i>	M				+							
Water Pipit <i>Anthus spinoletta</i>	M				+							
Loggerhead Shrike <i>Lanius ludovicianus</i>	V				+							
Western Meadowlark <i>Sturnella neglecta</i>	V				+							
Scott's Oriole <i>Icterus parisorum</i>	V				+							
Northern Oriole <i>Icterus galbula</i>	V				+							
Western Tanager <i>Piranga ludoviciana</i>	V				+							
Evening Grosbeak <i>Hesperiphona vespertina</i>	V					+						
Pine Siskin <i>Carduelis pinus</i>	M				+							
Black-throated Sparrow <i>Amphispiza bilineata</i>	V				+							

MONTIA LINEARIS (PORTULACACEAE): A NEW RECORD FOR UTAH

Stephen L. Clark¹ and Robert Graybosch¹

ABSTRACT.— *Montia linearis* Dougl., a plant known from British Columbia to Montana, Nevada, and California, is reported from Utah.

A collection of *Montia linearis* Dougl. by Buchanan 2135, Weber Co., Utah North Fork Park near Cobble Cr., 5600 feet, 9 July 1973 (WSCO) and distributed as *Montia chamissoi* (Ledeb) Dur. & Jacks. has been identified by Clark and Graybosch as *Montia linearis*. Collections of this plant by Clark 4150 from the

same general location July 1978 (WSCO) have further verified its existence in Utah. At present this is the only place in Utah where this plant is known to occur.

In Utah, this species should be considered rare, and endangered due to the heavy recreational use to which its habitat is subjected.

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FIRST RECORD OF THE SPOTTED BAT (*EUDERMA MACULATUM*) FROM OREGON

Ellen E. McMahon¹, Clifford C. Oakley², and Stephen P. Cross³

ABSTRACT.— A spotted bat (*Euderma maculatum*) was taken at Mickey Springs, 28 km northeast of Andrews, Harney County, Oregon. This represents a 225 km range extension and a new record for Oregon.

An adult female spotted bat (*Euderma maculatum*) was captured at Mickey Springs (T33S, R35E, S13) on 21 July 1976 at the north end of the Alvord Basin in southeastern Oregon. Mickey Springs, elevation 1235 m, and the Alvord Basin are located approximately 15 km east of Steens Mountain, 28 km northeast of Andrews, in Harney County. The rain shadow of Steens Mountain (elevation 2947 m) creates zeric conditions, and open water sources are scarce in the northern part of the basin. Mickey Springs itself is a hot spring, but its runoff forms a shallow, 12 x 24 m, cooled pond approximately 50 m to the east. This pond attracts numerous wildlife, including many bats. Mickey Mountain, elevation 1920 m, is located 3 km to the west and appears to be the closest area with potential roosting sites. The local vegetation is Shrub-Steppe (Franklin and Dyrness 1973), predominated by greasewood (*Sarcobatus vermiculatus*). Shadscale (*Atriplex confertifolia*) and sagebrush (*Artemisia tridentata*) are also abundant.

The spotted bat was captured sometime between midnight and 0800 in a mist net that had been tended for four hours after civil sunset and then furred to prevent further captures. The bat was discovered in a weakened condition as the net was being dismantled, and it subsequently died in the process of being removed from the net. It is on deposit in the Museum of Vertebrate Natural History at Southern Oregon State College, Ashland. External measurements are: total length, 124 mm; tail length, 49 mm; hind foot, 11 mm; ear, 41 mm; tragus, 15 mm; forearm, 52 mm; weight, 16.0 g.

This capture represents the first *Euderma* from Oregon. The closest record is from 24 km southwest of Caldwell, Idaho (Tucker, 1957), approximately 225 km northeast of Mickey Springs. Another *Euderma* was collected at Reno, Nevada (Hall 1935), 362 km to the south. These two marginal records and the similarity of habitat have led several authors (Hall and Kelson 1959, Snow 1973, Watkins 1977) to infer that the species range includes southeastern Oregon. Other species of bats captured at this site during four nights of netting were *Myotis leibii*, *Myotis volans*, *Lasionycteris noctivagans* and *Pipistrellus hesperus*.

We acknowledge the field assistance of Greg Gunson. Portions of the fieldwork were funded by the National Science Foundation, Student-Originated Studies Grant 76-07677.

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THE GREAT BASIN NATURALIST

Volume 41 No. 3

September 30, 1981

Brigham Young University



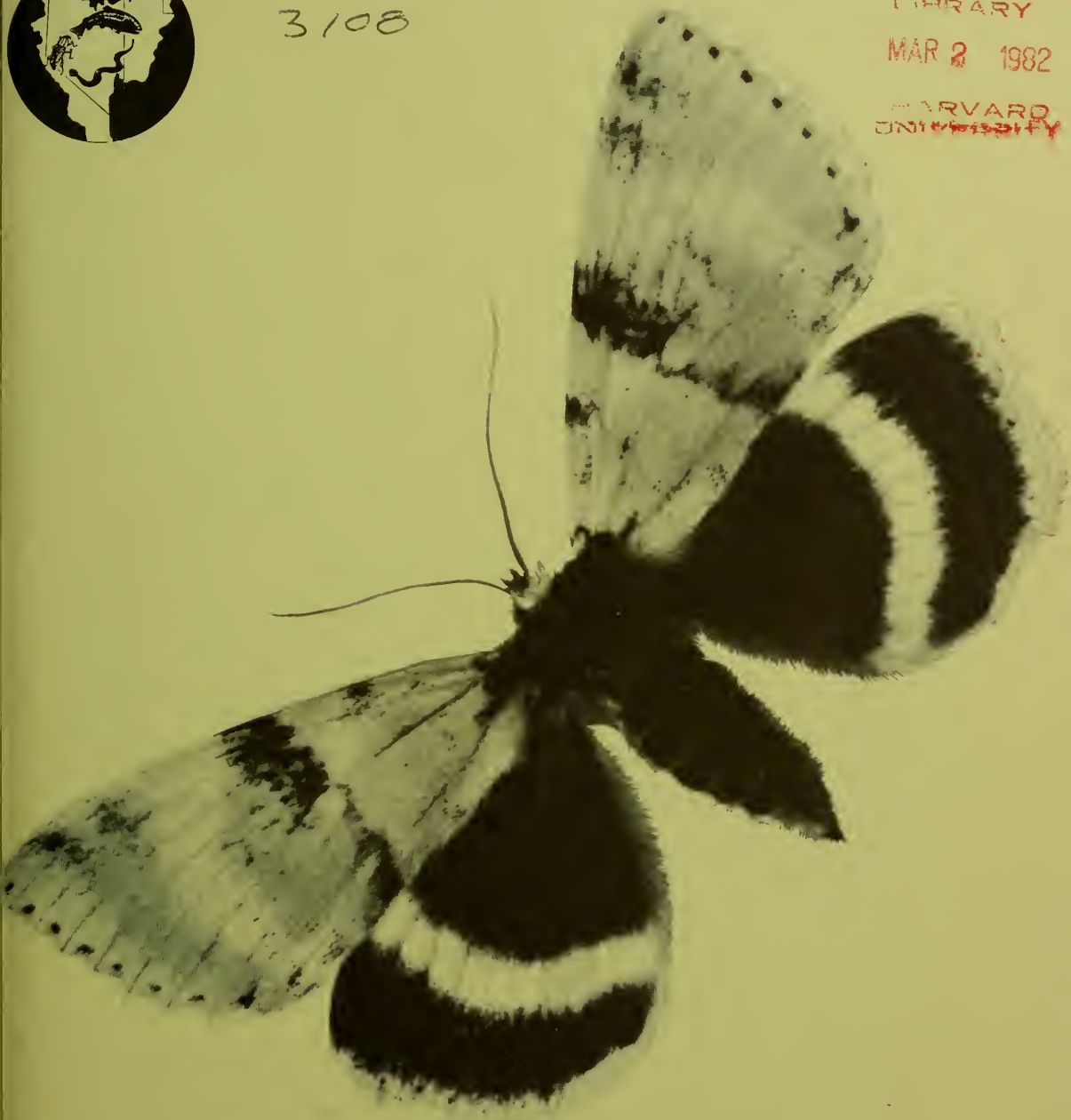
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The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 41

September 30, 1981

No. 3

LONG-TERM PLANT SURVIVAL AND DENSITY DATA FROM RECLAIMED SOUTHWESTERN COAL MINE SPOILS

Earl F. Aldon¹

ABSTRACT.— Plantings on northwestern New Mexico raw mine spoils from 1973, examined for establishment (1975) and survival (1979), showed 75 percent survival of fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.), each plant occupying 2.32 m² (1.52 × 1.52 m). Alkali sacaton (*Sporobolus airoides* (Torr.) Torr.) cover was 4 percent and had a density of 0.05 plant per m².

When the amount of strip mining of coal increased in the early 1970s in the Four Corners area of New Mexico, the biggest reclamation concern was whether plants could be reestablished at all on these low rainfall sites (Natl. Acad. Sci. 1974). Research and mining company reclamation specialists have shown that plant establishment of native species is both practical and feasible (Aldon 1975a, 1976, 1978). Nevertheless, we still do not know whether these reseeded plants survive and perpetuate themselves into stable ecosystems or how to manage these lands to maintain survival and stability.

This study addresses the survival question. Alkali sacaton and fourwing saltbush plants planted in 1973 on the Navajo Mine near Farmington, New Mexico, were measured in 1975 for establishment and in 1979 for survival. These two species were selected for testing based on previous research of their establishment requirements and their suitability to this site (Aldon 1970, 1975b). This paper presents the first comparisons of long-term survival data for these two species currently used in revegetation of southwestern mine sites.

Descriptions of the sites and planting treatments have been published (Aldon 1975a) and are felt to have little carryover value at this time. Briefly, the plantings were on untreated spoil material (no topsoil used) from the Watson Pit area of the Navajo Mine. The spoil is a dark, shale-derived material having the following characteristics:

Sand, percent	31
Silt, percent	27
Clay, percent	42
Textural class—clay	
Sodium absorption ratio (SAR)	44
Electrical conductivity × 10 ³	15
pH	7.7
Na (sol.) (meq/l)	175
Ca + Mg (meq/l)	31
N, kg/ha	146
P ₂ O ₅ , kg/ha	46
K ₂ O, kg/ha	380

The area surrounding the study area is rangeland with a scattering of low-growing shrubs. Principal grasses of the area include galleta (*Hilaria jamesii* (Torr.) Benth.), alkali sacaton, and Indian ricegrass (*Oryzopsis hymenoides* (R. + S.) Ricker). Shadscale (*Atriplex confertifolia* (Torr. + Frem.) Wats.), fourwing saltbush, and broadscale (*Atriplex*

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TABLE 1. Annual precipitation Navajo Mine Watson Pit study site.

Year	Winter	Growing season		Total (cm)
	December–April (cm)	May–November (cm)	July–August (cm)	
1974 ¹	6.38	8.84	1.14	15.22
1975	6.99	4.98	1.32	11.97
1976	2.29	8.81	5.69	11.10
1977	2.72	6.63	0	9.35
1978	14.15	8.13	0.25	22.28
1979	11.18	7.67	2.08	18.85
			Total	88.77
			Average annual	15.0

¹Record began September 1973.

obovata Moq.) are the most important shrub species. At higher elevations pinyons (*Pinus edulis* Engelm.) and junipers (*Juniperus* spp.) are found scattered on mesa tops. Elevation ranges from 1524 to 2000 m. Annual precipitation averages only 15 to 20 cm. Summer is usually wetter than winter; spring and fall are the drier seasons (Table 1). Temperatures may reach extremes of -32 to 44 C.

The planting treatments were (A) a direct seeding of fourwing saltbush without irrigation, (B) drip irrigated plantings of three-month-old fourwing saltbush transplants, (C) broadcast seeding of alkali sacaton on roto-tilled plots, and (D) seeding alkali sacaton in furrows. Both types of alkali sacaton seedings were sprinkler irrigated for the first growing season only (Aldon 1975a).

Five years after establishment, 62 percent of the fourwing saltbush plants on the A plots were alive and averaged 72.4 cm in height and 55.4 cm in diameter (Table 2). The plants were 14 percent shorter and 27 percent narrower than they had been five years earlier, probably due to plant competition,

because no grazing was present during this time. A live plant now occupies about 2.97 m², whereas a mature plant occupied about 1.86 m² two years after planting.

Survival of fourwing saltbush on B plots was 88 percent. Average plant height went from 62.2 cm in 1975 to 85.3 cm in 1979 and average plant diameter went from 59.7 cm to 98.3 cm (Table 2). Each live plant now occupies about 2.23 m².

Combining data from plots A and B, a fourwing saltbush plant occupies on the average 2.3 m² or an area 1.52 m × 1.52 m. Plant size and spacing seem to be related. Closely spaced plants were smaller and had large die-offs when compared with plants that were more widely spaced initially.

In 1979, on the C plots, there was an average of 36.8 surviving alkali sacaton plants. Average diameter was 10.16 cm. For mature plants the cover is 5.3 percent and density is 0.06 plants/m² (Table 3).

The D plots showed an average of 2.6 percent cover value. Using a plant count on the furrow plots, with a 10.16 cm average

TABLE 2. Survival and growth of fourwing saltbush.

Treatments	Live plants		Spacing		Average			
					Height		Diameter	
	A	B	A	B	A	B	A	B
			(m ² /plant)		(cm)		(cm)	
Measurement dates	#							
May 1973	400	— [*]	0.28	—			Seedlings	
September 1973	200	70	0.56	1.39			Seedlings	
July 1975	—	51	—	1.95	—	62.2	—	59.7
September 1975	60	—	1.86	—	82.3	—	75.7	—
May 1979	37	45	2.97	2.23	72.4	85.3	55.4	98.3
Percent survival (75–79)	61.7	88.2						

*— = measurement not taken

measured plant diameter, plant density was 0.04 plants/m².

Combining plots C and D, alkali sacaton averages 4 percent cover, 0.05 live mature plants per m² density.

These alkali sacaton densities are comparable to the 5.3 percent cover and 0.04 plants per m² found in three unmined semiarid pastures measured in another study, on the Rio Puerco watershed, near San Isidro, New Mexico, after two years of above average precipitation. The area, about 120 miles southeast of the present study site, normally receives about 24.1 cm of annual precipitation.

The potential for these two plants to reseed themselves on these sites is not fully understood. Moreover, complete understanding of mine spoil reclamation will have to be based on studies involving entire ecosystems over much longer periods of time. Nevertheless, these data give us some clues as to what plant densities can be established and sustained in this environment. Survival of these two species under difficult climatic and spoils conditions represents a significant start in the reclamation process on semiarid southwestern mined areas.

ACKNOWLEDGMENTS

We thank Utah International, Inc., for assistance in furnishing study areas, mechanized equipment, other facilities, and manpower for conducting the original field investigations. The research reported here is a contribution to the SEAM program. SEAM, an acronym for Surface Environment and

TABLE 3. Alkali sacaton plant density and cover.

Treatment	Density 1975 (seedlings/ m ²)	Density 1979 (plants/m ²)	Cover 1979 (%)
C	0.36	0.06	5.3
D	0.29	0.04	2.6

Mining, is a Forest Service program to research, develop, and apply technology that will help maintain a quality environment and other surface values while helping meet the nation's mineral requirements.

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VIABILITY OF SEED FROM THIRTY-TWO SHRUB AND FORB SPECIES THROUGH FIFTEEN YEARS OF WAREHOUSE STORAGE

Richard Stevens¹, Kent R. Jorgensen¹, and James N. Davis¹

ABSTRACT.— Germination results were obtained from seed stored in an open warehouse in Sanpete County, Utah, over a 15-year period for 18 shrub and 14 forb species. Seed viability was not appreciably affected for 14 species stored at least 15 years. Seed viability did, however, significantly decrease for two species stored 10 years, for five species stored 7 years, for seven species stored 5 years, for three species stored 4 years, and for one species stored only 3 years.

A major limiting factor in range rehabilitation and improvement projects is the availability of seed of wildland species. Seed of most native shrub and forb species used in habitat improvement projects is available only from wildland sources and must be collected by hand. Lack of adequate soil moisture during critical flowering and seed development periods, frost, insect infestation, or other natural causes prevent yearly production of good seed crops. Seed is high priced or unavailable in years of low production. To have on hand adequate seed when needed at reasonable cost, seed must be stockpiled. In a seed storage program, it becomes imperative to know the maximum length of time each species can be stored and still retain appreciable amounts of viability.

Comprehensive germination studies have been done with a number of species using seed from the collection year. Germination of the seed of some agricultural crops and grasses stored a number of years has been studied extensively (Hafenrichter et al. 1965, Little 1937, Tiedemann and Pond 1967), but germination studies of wildland shrubs and forbs have been limited. Springfield (1968, 1970, 1973, 1974) worked with germination and longevity of stored winterfat and four-wing saltbush seed. Longevity reports on germination of stored winterfat (Stevens et al. 1977) and bitterbrush seed (Giunta et al. 1978) also have been made.

Plummer et al. (1968) lists the duration of good viability for 44 shrubs, 24 forbs, and 5 grasses. A report on results after relatively

short periods of storage on seed of a number of native shrubs and forbs was made by Plummer et al. (1970). Two works including information on germination and longevity studies for many native trees and shrubs were published by the USDA Forest Service (1948, 1974).

Wildland seed is commonly stored in unheated and uncooled warehouses and granaries, sometimes for extended periods of time, and little information is available as to the length of life of stored seed.

METHODS

During the fall of 1963, seed of 18 shrub and 14 forb species (Table 1) were hand collected from native stands. Seed was hand cleaned to 85 percent purity or higher, placed in cotton bags, and deposited in metal file cabinets in an open, unheated, and uncooled warehouse in Ephraim, Sanpete County, Utah, for the duration of the study. Over 15 years (1963 through 1978), temperature in the warehouse ranged from a low of -29.9°C (-21°F) to a high of 38.3°C (101°F). Mean daily temperatures during winter, spring, summer, and fall periods were -3.3°C (26°F), 6.7°C (44°F), 20°C (68°F), 7.2°C (45°F), respectively.

Germination tests began in February of 1965, 1966, 1967, 1968, 1970, 1973, and 1978. These years marked the beginning of the 2nd, 3rd, 4th, 5th, 7th, 10th, and 15th year of storage. For each species in each year of sampling, four random samples of 100

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seeds each were selected and individually placed between damp newspapers, wrapped in plastic, and placed in a refrigerator. Temperature in the refrigerator ranged between 1.1 and 3.3 C (34 and 38 F). Care was taken to ensure that only undamaged seed with good fill was selected and used. Results then were based on over 98 percent fill and 100 percent purity for all species except fourwing saltbush (52 percent fill) and Martin ceanothus (59 percent fill). Seed samples were checked at 14-day intervals. All germinated seeds were removed and the number germinated was recorded. Seed samples remained in an unlighted refrigerator, and germination checks were made on schedule for up to 16 months. Seeds were considered germinated when the hypocotyl length reached 5 mm.

Analysis of variance and Newman-Keul's (Steel and Torrie 1960) comparison of mean test (0.05 level of significance) was used to determine where germination significantly changed.

RESULTS AND DISCUSSION

There is a possibility that up to 16 months of incubation at temperatures ranging from 1.1 to 3.3 C (34 to 38 F) in cool, moist stratification may increase germination for some species above what can be expected from field seedbeds.

In 10 species, percent germination did not drop significantly over 15 years of storage. Silky lupine maintained the highest germination with an overall mean of 94 percent (Table 1); germination means of small burnet, Nevada ephedra, green ephedra, cliffrose, and antelope bitterbrush did not drop significantly over 15 years, and all were between 79 and 94 percent. Overall mean germination of curleaf mountain mahogany remained at 70 percent and that of fourwing saltbush did not vary significantly through 15 years. Gooseberry globemallow germination had an overall germination mean of 7 percent over the 15-year test period. Martin ceanothus had a mean for the first 7 years of only 7 percent; with 10 and 15 years of storage, germination increased to a mean of 38 percent. This could possibly be explained because insect-damaged seed was more easily recognized when samples were selected later in the study.

By the 15th year of storage, percent seed germination of desert bitterbrush, Saskatoon serviceberry, Utah serviceberry, and Palmer penstemon had decreased significantly but was still at acceptable levels for each species. Percent germination for desert bitterbrush ranged from a high of 86 percent down to 65 percent, Saskatoon serviceberry from 91 to 76 percent, Utah serviceberry from 99 to 67 percent, and Palmer penstemon from 83 to 50 percent. Lewis flax germination dropped off significantly after the 10th year of storage. Between the 7th and 10th year of storage, seed of squawapple lost almost 50 percent of its viability, going from 39 percent germination to 21 percent. Seed of showy goldeneye also decreased between the 7th and 10th year, dropping from 13 percent to only 1 percent germination.

From the 5th to the 7th to the 10th year of storage, germination percent in true mountain mahogany seed dropped from 68 to 46 to 25 percent. Percent germination of vegetable oyster salsify seed decreased from 66 to 46 to 31 percent by the 10th year of storage and that of mountain snowberry went from 80 percent the 7th year to 44 percent the 10th year, to 8 percent after 15 years of storage.

Significant decrease in percent germination occurred between the fifth and seventh years of storage of basin big sagebrush seed (70 to 24 percent), spineless hopsage (57 to 13 percent), arrowleaf balsamroot (37 to 20 percent), Porter ligusticum (36 to 13 percent), Utah sweetvetch (55 to 25 percent), Wyeth eriogonum (90 to 64 percent), and cutleaf balsamroot (20 to 4 percent).

Four years of storage appears to be the point at which seed viability drops significantly for winterfat, black sagebrush, white rubber rabbitbrush, and five years for Nuttall lomatium. Seven and 8 percent germination was obtained in two- and three-year-old cowparsnip seed, but only 2 percent was recorded after four years' storage.

Checks on seed of antelope bitterbrush, cliffrose, Lewis flax, and Porter ligusticum showed that percent germination significantly increased with two to three years of storage, an indication that these species may have afterripening periods.

TABLE 1. Mean percent germination* of seed from 32 shrub and forb species after 2, 3, 4, 5, 7, 10, and 15 years storage in an open, unheated, and uncooled warehouse.

Species	Source	Years of storage						
		2	3	4	5	7	10	15
Percent germination								
Shrubs								
Antelope bitterbrush (<i>Purshia tridentata</i>)	Mt. Dell, Utah	79	86	87	94	88	88	85
Basin big sagebrush (<i>Artemisia tridentata tridentata</i>)	Ephraim, Utah	73	82	67	70	24	1	0
Black sagebrush (<i>Artemisia nova</i>)	Manti, Utah	81	66	55	34	5	1	0
Cliffrose (<i>Cowania mexicana stansburiana</i>)	American Fork, Utah	80	89	—	89	84	89	91
Curleaf mountain mahogany (<i>Cercocarpus ledifolius</i>)	Mayfield, Utah	67	63	—	80	76	69	64
Desert bitterbrush (<i>Purshia glandulosa</i>)	Bishop, California	78	86	80	80	69	73	65
Fourwing saltbush (<i>Atriplex canescens</i>)	Panaca, Nevada	32	47	40	40	50	43	37
Green ephedra (<i>Ephedra viridis</i>)	Manti, Utah	88	92	92	84	80	82	88
Martin ceanothus (<i>Ceanothus martinii</i>)	Manti Canyon, Utah	3	5	5	12	10	40	36
Mountain snowberry (<i>Symphoricarpos oreophylicus</i>)	Spanish Fork Canyon, Utah	80	64	—	92	80	44	8
Nevada ephedra (<i>Ephedra nevadensis</i>)	Wah-Wah Valley, Utah	90	93	91	85	89	91	85
Saskatoon serviceberry (<i>Amelanchier alnifolia</i>)	Spring City Canyon, Utah	91	80	—	91	85	84	76
Spineless hopsage (<i>Grayia brandegei</i>)	Escalante, Utah	87	92	86	57	13	6	0
Squawapple (<i>Peraphyllum ramosissimum</i>)	New Canyon, Utah	42	42	42	37	39	21	10
True mountain mahogany (<i>Cercocarpus montanus</i>)	New Canyon, Utah	63	65	61	68	46	25	3
Utah serviceberry (<i>Amelanchier utahensis</i>)	Henrieville, Utah	97	99	—	99	96	90	67
White rubber rabbitbrush (<i>Chrysothamnus nauseosus albicaulis</i>)	Richfield, Utah	80	65	34	14	11	7	0
Winterfat (<i>Ceratoides lanata</i>)	Corona, New Mexico	90	83	74	18	7	0	0
Forbs								
Arrowleaf balsamroot (<i>Balsamorhiza sagittata</i>)	Paradise Valley, Nevada	40	42	—	37	20	1	0
Cowparsnip (<i>Heracleum lanatum</i>)	Pleasant Creek Canyon, Utah	7	8	2	1	0	0	0
Cutleaf balsamroot (<i>Balsamorhiza macrophylla</i>)	Bountiful, Utah	35	28	17	20	4	0	0
Gooseberry globemallow (<i>Sphaeralcea grossulariaefolia</i>)	Benmore, Utah	7	7	6	9	6	7	6
Lewis flax (<i>Linus lewisii</i>)	Ephraim, Utah	66	72	85	93	83	70	25
Nuttall lomatium (<i>Lomatium nuttallii</i>)	Ephraim Canyon, Utah	69	73	—	73	37	8	2
Palmer penstemon (<i>Penstemon palmeri</i>)	Ephraim Canyon, Utah	83	81	—	80	79	65	50
Porter ligusticum (<i>Ligusticum porteri</i>)	Ephraim Canyon, Utah	11	28	24	36	13	0	0
Showy goldeneye (<i>Viguiera multiflora</i>)	Ephraim Canyon, Utah	18	17	11	18	13	1	0

*Results based on 98 percent or better fill and 100 percent purity, except fill for fourwing saltbush (52 percent fill) and Martin ceanothus (59 percent fill).

Table 1 continued.

Species	Source	Years of storage						
		2	3	4	5	7	10	15
Percent germination								
Silky lupine (<i>Lupinus sericeus</i>)	Ephraim Canyon, Utah	97	99	100	99	86	85	92
Small burnet (<i>Sanguisorba minor</i>)	Ephraim, Utah	88	93	91	96	82	87	88
Utah sweetvetch (<i>Hedysarum boreale germinale</i>)	Orem, Utah	59	67	58	55	25	40	16
Vegetable oyster salsify (<i>Tragopogon porrifolius</i>)	Mt. Pleasant, Utah	65	65	66	66	46	31	13
Wyeth eriogonum (<i>Eriogonum heracleoides</i>)	Brigham City, Utah	51	87	—	90	64	16	5

SUMMARY

Germination results from seed stored over a 15-year period indicate that seed of fourwing saltbush, curleaf mountain mahogany, cliffrose, Nevada and green ephedra, antelope bitterbrush, silky lupine, small burnet, Martin ceanothus, and gooseberry globemallow can be stored at least 15 years without any significant loss in percent germination. Results indicate that seed of Palmer penstemon, Utah and Saskatoon serviceberry, and desert bitterbrush start to lose viability by the 15th year of storage. Ten years appears to be a maximum storage period for seed of mountain snowberry and Lewis flax. Where reasonable germination is expected, storage exceeding 7 years is not recommended for seed of true mountain mahogany, squawapple, showy goldeneye, vegetable oyster salsify, and Wyeth eriogonum. Storage longer than 5 years results in a significant drop in seed viability of basin big sagebrush, spineless hopsage, arrowleaf and cutleaf balsamroot, Porter ligusticum, Nuttall lomatium, and Utah sweetvetch.

Four years is the maximum storage period recommended for seed of black sagebrush, winterfat, and white rubber rabbitbrush. Maximum storage of cowparsnip seed should not exceed three years.

ACKNOWLEDGMENTS

Funds were provided through Federal Aid in Wildlife Restoration Project W-82-R (Job IV) and USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.

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CONTRIBUTIONS TO THE LIFE HISTORY OF SACRAMENTO PERCH, *ARCHOPLITES INTERRUPTUS*, IN PYRAMID LAKE, NEVADA

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ABSTRACT.— During a two-year period (1976–1977), 180 Sacramento perch (*Archoplites interruptus*) were sampled from Pyramid Lake, Nevada, on a monthly basis using several capture methods in all lake areas. Age and growth determinations of these fish were inconsistent with previous research on this species. Sacramento perch are entirely carnivorous, adults feeding primarily on tui chub (*Gila bicolor*). Fish accounted for 6 percent of the diet (by volume) of Sacramento perch less than 300 mm fork length, and 98 percent for those exceeding 300 mm. Amphipods, Odonata, and Chironomidae composed 6.3, 5.7, and 1.8 percent, respectively, of the stomach contents by volume for all sizes combined. Females spawned from June to August when water temperatures approached 20 C, and their gonad weight was about 6 percent of the total body weight. A sample of 20 female perch had a mean fecundity of 84,203 eggs. The mean diameter of mature eggs was 0.88 mm. Sacramento perch almost exclusively inhabit the littoral zone of Pyramid Lake. Activity, as indicated by net catches, was greatest during the warm months of May to October. Monthly catches were significantly correlated with temperature ($r = 0.577$, $P < 0.01$). No short-term changes in population abundances were observed during 1976–1977.

The Sacramento perch is the only warm water gamefish in Pyramid Lake. Its preference for warm, shallow water makes it available to shore as well as boat fishermen during the hottest months of the year, when trout are relatively inaccessible. Although not abundant, the Sacramento perch supports a limited summer fishery and is an excellent food fish. An analysis of an aboriginal fishing site in central California indicated that Sacramento perch was the most abundantly utilized species (51 percent of the remains) by the prehistoric Native Americans (Schulz and Simons 1973). In 1931 Walford noted that the Sacramento perch was esteemed by anglers. In recent years interest has been renewed in this fish both as a game fish and as a candidate for the list of endangered species (Aceituno and Nicola 1976). It is currently classified as depleted (Miller 1972).

The Sacramento perch is the only member of the sunfish (Centrarchidae) family naturally distributed west of the Rocky Mountains (Murphy 1948). It is the only living member of the genus *Archoplites*, a relict of an ancient fauna that probably evolved before the formation of the Sierra Nevada and Rocky Mountain ranges (Miller 1946, 1958,

1959). The species is endemic to the Sacramento-San Joaquin drainage systems of California (Aceituno and Nicola 1976) (Fish). Sacramento perch probably attained present distribution during the Miocene epoch, some 25 million years ago (Miller 1959). The occurrence of fossil *Archoplites* in ancient Lake Idaho suggests a former geographic connection between what are now the Snake River and Sacramento River drainages (Miller and Smith 1967).

Lockington (1879) described the Sacramento perch population of the lower Sacramento and San Joaquin Rivers as being abundant in the late 1800s. Nevertheless, the species was noted to be declining in its native range before the turn of the century (Jordan and Evermann 1896). After the turn of the century it was considered uncommon (Rutter 1908), and by the end of the 1940s it was considered scarce, except in a few isolated localities (Murphy 1948, Curtis 1949). By 1955 the Sacramento perch was occupying only a fraction of its original range in California, being limited to 14 small and disjunct bodies of water (Aceituno and Nicola 1976). The decline of Sacramento perch in its native habitat has been attributed to predation, habitat

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Fig. 1. Original distribution of Sacramento perch (after Aceituno and Nicola 1976).

degradation, interspecific competition for food and space, and reduced abundance of native cyprinid prey (Jordan and Gilbert 1895, Neale 1931, Dill and Shapovalov 1939, Murphy 1948, 1951, Mathews 1962, Hopkirk 1973, Moyle et al. 1974). Aceituno and Nicola (1976) discuss these relationships in detail and suggest that competition from introduced exotic centrachids is a probable cause of the demise of Sacramento perch in California.

As Sacramento perch began declining in their native range, they were introduced into other waters. H. G. Parker (first fish commissioner of the State of Nevada) planted Sacramento perch from the Sacramento River into Washoe Lake in 1877 (LaRivers 1962). The species was subsequently distributed to other waters of Nevada, including Pyramid and Walker Lakes. By 1897 a relatively large population of Sacramento perch had apparently been established in Pyramid Lake,

because Fish Commissioner G. T. Mills reported a commercial Indian fishery for the species (LaRivers 1962). Aceituno and Nicola (1976) summarized efforts to reestablish Sacramento perch in California waters. They noted that nearly all the waters where Sacramento perch now exist in California are artificial introductions, i.e., the species is virtually nonexistent in its original range.

AGE AND GROWTH

Age data, in conjunction with length and weight measurements, comprise an important aspect of fisheries biology because it provides information on stock composition, age at maturity, life span, mortality, growth, and production (Tesch 1971). This information is relevant to ecological relationships of a fish species living in various habitats. The most frequently used method of age determination in a temperate region is the measurement and interpretation of growth zones on the hard parts of fishes, particularly, scales. The classic aging techniques used in this study were not definitive for Sacramento perch. Annual growth increments of 104 Sacramento perch taken from Pyramid Lake during 1976–1977 exhibited a different pattern than had been previously reported for the species from Pyramid Lake and other waters (Table 1). The back-calculated length of Sac-

ramento perch at time of first annulus formation during this study (137–244 mm) is comparable to the length reported at the second or third annulus of Sacramento perch sampled from Pyramid Lake by Johnson (1958) and Mathews (1962) and from Walker Lake by Allan (1958). The mean annual growth increments (in length) of Sacramento perch collected in 1959 by Mathews (1962) were, however, much greater than those calculated during this study. If, however, our 1976–1977 data are adjusted to make the length at first annulus (males) or first and second annuli (fe males) equal to that of Mathews (1962), then the subsequent annual growth increments are more comparable between the two time periods (Table 2). Such an adjustment, partitioning out the length at first annulus into the proportion determined by Mathews (1962), is arbitrary, but it suggests possible explanations of the ambiguous results: (1) the first annulus may be obscured or not laid down the first year, (2) a true annulus was interpreted as a check mark and disregarded, and (3) previous workers interpreted actual check marks as true annuli. Annulus formation is probably a function of food availability and temperature in Pyramid Lake. Sacramento perch are spawned late in the year in Pyramid Lake due to the relatively slow warming of the water (Mathews 1962). Following scale formation

TABLE 1. Comparison of Sacramento perch growth from different California and Nevada waters.

Locality	Calculated mean fork length (mm) at each annulus								
	1	2	3	4	5	6	7	8	9
California									
Lake Greenhaven (Mathews 1962)	84	163	203	239	286	312			
Lake Almanor (Mathews 1962)	59	122	172	198	217	282			
Lake Anza (Mathews 1962)	86	120	131	138	147	154			
King Fish Lake (Mathews 1962)	115	—	—	—	—	—			
Clear Lake (Murphy 1948)	85	171	196	220					
Nevada									
Walker Lake (Allan 1958)	102–127	140–190	190–241	229–299	279–318	305–356			
Pyramid Lake (Johnson 1958)	76–127	127–190	178–254	229–305	279–343	305–356	324–368	381–398	314–400
Pyramid Lake (Mathews 1962)	99	158	221	261	299	325	346	371	382
Pyramid Lake (This study)	137–224	186–267	219–300	252–333	312–355				

TABLE 2. Annual growth increments of Sacramento perch sampled from Pyramid Lake during 1959 and 1976-1977.

Age	1959 (Mathews 1962)		1976-1977			1976-1977 adjusted ¹
	Females	Males	Females	Males	Females	Males
I	105	91	213	160	105 ²	91 ²
II	58	60	42	58	58 ²	69
III	64	61	34	49	50	58
IV	44	30	30	37	42	49
V	39	24	20	—	34	37
VI	25	16	—	—	30	—
VII	18	22	—	—	20	—
VIII	24	34	—	—		
IX	23	11	—	—		

¹Assuming 1976-1977 growth at first annuli (males) or first and second annuli (females) were equal to Mathews's (1962) determinations.

²Mathews's (1962) data.

(July-August), therefore, the growing season probably only encompasses 1-4 months. If the time of optimum growth extended for a month or less, the first annulus could be close enough to the focus to be obscured. During years of exceptionally late spawning and/or early winters, the young-of-year may overwinter before scale formation occurs, i.e., at a length of <54 mm. If the fish had actually completed two years of life before the first annulus was discernible, it would help explain why the age determined for the 1976-1977 collections was so much younger than had been previously reported for Sacramento perch from Pyramid Lake and other waters. No individuals aged at more than five years were sampled during 1976-1977. Mathews (1962) and Johnson (1958) both reported Sacramento perch through age IX from Pyramid Lake.

Growth zones regarded as false annuli or check marks were frequently encountered during this study. Scale circuli were determined to be true annuli by applying the criteria described by Aceituno and Vanicek (1976). Because we are unable to resolve apparent inconsistencies in the aging method-

ology, however, further interpretation of these data will not be presented.

The length-weight relationship for Sacramento perch is curvilinear (Fig. 2) and is best described by an exponential or logarithmic linear equation (Table 3). The slope of the logarithmic regression equation represents the rate of weight accrual for given lengths. In Pyramid Lake, our results indicated that female Sacramento perch (slope = 2.726) grow more rapidly than males (slope = 2.560) throughout life.

Coefficients of condition ($K = W \times 10^5/L^3$) were computed for 103 Sacramento perch. The condition factor of females averaged slightly higher than that of males (Table 4). This indicates that females were heavier than males per given length. With the exception of the young-of-the-year fish, the K-values generally decreased as length and age increased. K-values ranged from 1.165 and 2.759, with a mean of 1.965.

FOOD HABITS

The diet of 42 Sacramento perch from Pyramid Lake was determined during 1976. The fish ranged between 203-376 mm in fork

TABLE 3. Regression equations of fork length (L) in centimeters versus weight (W) in grams, of 103 Sacramento perch taken from Pyramid Lake, Nevada, April 1976-November 1977.

Sex	Sample size (n)	Exponential	Logarithmic
Male	30	$W = .0840 L^{2.5602}$ ($r^2 = .90$)	$\log_{10}W = -1.076 \times 2.560 \log_{10}L$ ($r^2 = .90$)
Female	59	$W = .0534 L^{2.7257}$ ($r^2 = .92$)	$\log_{10}W = -1.272 \times 2.726 \log_{10}L$ ($r^2 = .92$)
Combined (including indeterminate)	103	$W = .0144 L^{3.0935}$ ($r^2 = .96$)	$\log_{10}W = -1.841 \times 3.094 \log_{10}L$ ($r^2 = .96$)

length. The specimens were captured in-shore, on the bottom at depths of 0-15 in various lake areas during all seasons. The 12 empty stomachs (28.6 percent) were seen from May through August, and may have been due to regurgitation.

TABLE 4. Average length (mm), weight (g), and condition factors of female and male Sacramento perch collected in Pyramid Lake, Nevada, from 1975 to 1977.

Length groups	Number of fish	Mean length (mm)	Mean weight (g)	Mean K
Female				
100-150	1	142	79	2.759
150-200	0	—	—	—
200-250	0	—	—	—
250-300	6	280	500	2.223
300-350	43	326	708	2.037
350-400	9	370	1061	2.078
Male				
100-150	2	143	72	2.478
150-200	0	—	—	—
200-250	2	236	250	1.902
250-300	14	276	432	2.099
300-350	12	326	627	1.810

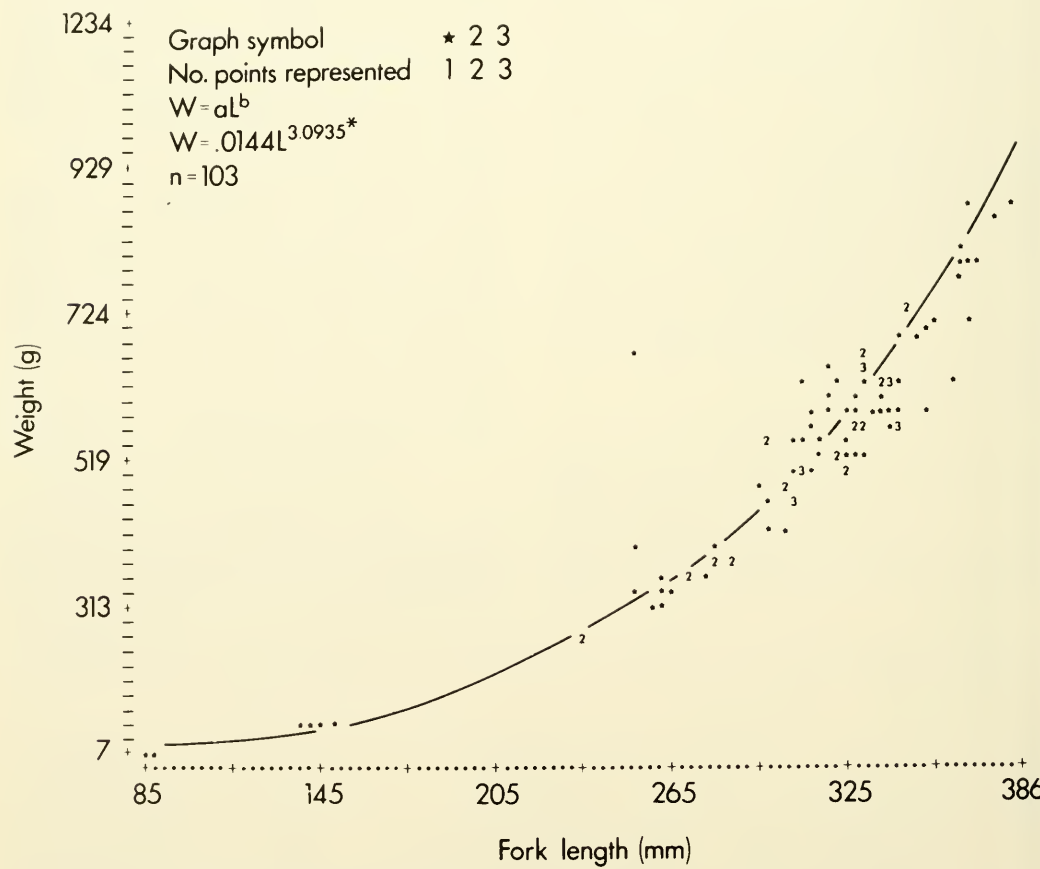


Fig. 2. Length-weight relationship of combined data for Sacramento Perch collected from April 1976 to November 1977, Pyramid Lake, Nevada. Mean length-weight values by age group are presented.

Food items in the Sacramento perch stomachs were separated into six categories: fish, Odonata, Chironomidae, Amphipoda, algae, and digested matter. Fish had been eaten by 65.6 percent of the Sacramento perch whose stomachs contained food and accounted for nearly 86 percent of the total volume of stomach contents (Table 5). Johnson (1958) reported that 49 of 54 (90 percent) of the Pyramid Lake Sacramento perch containing food in their stomachs had eaten fish. In Walker Lake, Allan (1958) determined that 110 of 164 (67 percent) of the Sacramento perch containing food in their stomachs had eaten fish. This piscivorous nature of Sacramento perch has been well documented (Neale 1931, Murphy 1948, Jonez 1955, LaRivers 1962, Mathews 1962, Sigler and Miller 1963).

During this study, all fish identified from stomachs of Sacramento perch were tui chubs. Johnson (1958) also found Sacramento perch from Pyramid Lake to predominantly contain tui chub minnows 25–127 mm in length, and Allan (1958) stated that all identifiable fish from stomachs of Sacramento perch in Walker Lake were tui chubs 38–178 mm in length. Moyle et al. (1974) and Mathews (1962) found tui chubs, Tahoe suckers, and other Sacramento perch in the stomachs of Sacramento perch from Pyramid Lake.

The proportion of fish in the diet increases as the size of the Sacramento perch increases (Table 6). Only 3 of 11 Sacramento perch 203–292 mm in length had eaten fish, whereas 17 of 19 perch measuring over 300 mm had fish in their stomachs. The percentage of

fish in the total food volume of Sacramento perch from the two groups is even more striking. Fish amounted to only 6 percent of the volume for Sacramento perch less than 300 mm in length, but 98 percent for those exceeding 300 mm. Moyle et al. (1974) and Mathews (1962) noted a transition from invertebrates to fish in the diet of Sacramento perch at a much smaller size, i.e., Sacramento perch over 90 mm in fork length sampled during July 1961 from Pyramid Lake contained over 90 percent fish, by weight, in their stomach contents. This discrepancy may be partially explained by depth of habitat sampled. Fish in this study were captured in gill nets up to a depth of 15 m. Mathews (1962) primarily used minnow seines (also rotenone and angling), which restricted sampling to relatively shallow areas where small forage fish are more available for predation.

Odonata comprised nearly 42 percent of the benthic invertebrates in stomachs of Sacramento perch. They accounted for 5.7 percent of total Sacramento perch food and had been eaten by 13.3 percent of the specimens examined. Odonata are relatively abundant in the tufa and rock areas of Pyramid Lake inhabited by adult Sacramento perch. Chironomidae had been eaten by 9 of 30 Sacramento perch examined and composed 1.8 percent of the total volume. As Sigler and Miller (1963) observed, Sacramento perch of all sizes feed on Chironomidae. Chironomidae were consumed throughout the year but in the largest volumes during May, June, and July. Amphipoda had been eaten by 20 percent of the Sacramento perch (mostly small fish) and accounted for 6.3 percent of the total volume

TABLE 5. Stomach contents of 30 Sacramento perch (203–376 mm fork length) from Pyramid Lake, Nevada, during 1976.

Food item	Frequency	Percentage frequency of occurrence	Volume in cc	Percentage of total volume	Percentage of total volume excluding digested matter
Fish	20	66.67	96.5	85.93	81.16
Amphipoda	6	20.00	7.1	6.32	6.34
Odonata	4	13.33	6.4	5.70	5.71
Chironomidae	9	30.00	2.0	1.78	1.79
Algae	1	3.33	Trace*	Trace*	Trace*
Digested matter	2	6.67	0.3	0.27	—
Total	—	—	112.3	100.00	100.00

*Trace = less than 0.1.

of food. Mathews (1962) also observed that small (49–77 mm) Sacramento perch fed heavily on amphipods (71.7 percent of the diet), and larger Sacramento perch depended much less on benthic invertebrates (6.3 percent of the diet), of which odonata were the most important constituent.

The feeding behavior of Sacramento perch in Pyramid Lake is not known in detail. Moyle et al. (1974) concluded from stomach analyses that Sacramento perch fed primarily by picking invertebrates off the bottom substrate or by capturing organisms in midwater. LaRivers (1962) characterized Sacramento perch as "lurkers," hiding in rocky crevices, apparently in wait for passing prey. In Pyramid Lake, the convoluted habitat of tufa formations, combined with huge schools of tui chubs in shallow water, would make the lurking method of predation efficient for any piscivorous fish.

Sacramento perch can be categorized as a stenophagous species, i.e., they subsist on a limited variety of foods. Sacramento perch are entirely carnivorous, becoming almost totally piscivorous when they attain a large enough size. Their macroinvertebrate prey are restricted to benthic species that cohabit in shallow rocky areas. The great abundance and availability of all sizes of tui chubs inshore during the summer months make them

the preferred food of Sacramento perch large enough to consume fish. The highest Sacramento perch predation on fish occurred during May–August when adult tui chubs were inshore spawning and young-of-the-year tui chubs were present in high numbers. Mathews (1962) examined 216 Sacramento perch from Lake Anza, California, and showed the highest occurrence of predation on fish to occur from May–September.

REPRODUCTION

Sacramento perch ripen and spawn in various bodies of water at temperatures ranging from 20.0 to 23.9 C (Murphy 1948, Mathews 1962, 1965, McCarraher and Gregory 1970, Imler et al. 1975, Aceituno and Vanicek 1976). In Pyramid Lake, Sacramento perch spawn from June through August, beginning when water temperatures approach 20 C. Collection of young-of-the-year perch in late July and August 1976, when water temperatures were 21.1 to 22.2 C, further delineated Sacramento perch's spawning season in Pyramid Lake. The highest net catch rate of adult Sacramento perch in spawning condition was observed at the delta early in August; relatively large numbers of postlarval Sacramento perch were seined in this area by the end of the month. Female Sacramento perch

TABLE 6. Percentage of total volume and frequency of occurrence of food items consumed by Sacramento perch in relation to size. Perch were captured from January through December 1976 from Pyramid Lake, Nevada, with bottom-set horizontal gill nets.

Food item	Volume	Percent of total volume	Frequency by occurrence	Frequency of occurrence by percent
Size group 203–292 mm (n = 11)				
Fish	0.9	6.08	3	27.27
Amphipoda	5.8	39.19	4	36.36
Odonata	6.3	42.57	3	27.27
Chironomidae	1.5	10.14	6	54.55
Algae	Trace*	Trace*	1	9.09
Digested matter	0.3	2.03	2	18.18
Mean fork length = 255 mm		Mean weight = 390 g		
Range = 203–292 mm		Range = 177–830 g		
Size group 300–376 mm (n = 19)				
Fish	95.6	98.05	17	89.47
Amphipoda	1.4	1.44	2	10.53
Odonata	0.1	0.10	1	5.26
Chironomidae	0.4	0.41	3	15.79
Mean fork length = 326 mm		Mean weight = 735 g		
Range = 300–376 mm		Range = 544–1,148 g		

*Trace = less than 0.1.

spawn when their gonad weight is about 6 percent of the total body weight. In 1976, this GSI was reached during July and August. Shallow littoral areas with substrates of gravel, boulders, algae, and/or rooted aquatic plants are characteristic spawning habitats of Sacramento perch (Murphy 1948, Mathews 1965, McCarraher and Gregory 1970). Spawners are generally paired, and they exhibit increasingly aggressive behavior that culminates in egg deposition in which both fish are often vertically positioned with the vents close together (Murphy 1948). The eggs are formed in long adhesive strings laid conspicuously over a discrete area of substrate about 0.5 m in diameter. Unlike other centrarchids, Sacramento perch exhibit little if any nest-building behavior (McCarraher and Gregory 1970). After completion of spawning, the male may (Mathews 1965) or may not (Miller 1948) display nest-guarding territoriality for several days. Presence or absence of this protective behavior would certainly affect reproductive success. Scuba diving observations indicate that Sacramento perch exhibit nest-guarding territoriality in Pyramid Lake.

Although actual spawning of Sacramento perch in Pyramid Lake was not observed during this study, tufa formations probably provide suitable spawning substrate. Net catches of young-of-the-year Sacramento perch in the vicinity of the pinnacles and the delta attest to successful reproduction in these areas. The abundant wind-blown tumbleweed in Pyramid Lake may also provide spawning substrate; this plant was utilized by Sacramento perch in White Lake, South Dakota (McCarraher and Gregory 1970).

Natural recruitment of Sacramento perch in Pyramid Lake has apparently resulted in maintenance of a stable population since the fish was first introduced in the late 1800s. The delta area may be an important nursery area for Sacramento perch, because the largest catch of postlarval juveniles was taken in this area. Eggs and young probably have higher survival rates in the vicinity of Truckee River inflow due to reduced total dissolved solids (TDS) levels. Fry and fingerling Sacramento perch are less tolerant of high TDS than adults, and apparently a mortality threshold greatly reduces the survival

of fry to maturity (McCarraher and Gregory 1970). Sacramento perch successfully reproduced in saline Colorado ponds ranging from 1,000–19,000 mg/l TDS, with total alkalinity less than 400 mg/l (Imler et al. 1975). It is generally conceded, however, the alkalinity (carbonates-bicarbonates) and not salt (NaCl) is the TDS constituent harmful to fish (Beatty 1959, Mitchum 1960).

Alkalinity may also directly affect the reproductive potential of adult Sacramento perch and is probably the mechanism that eliminated this species from Walker Lake. Walker Lake's now extinct Sacramento perch reached their limit of "alkalinity" tolerance when they could no longer reproduce in the early 1950s, when the total alkalinity was approximately 2,500 mg/l as HCO_3^- (Cooper 1978). Natural reproduction did not occur in Nebraska hatchery ponds unless the total alkalinity was less than 2,000 mg/l over the summer months (McCarraher and Gregory 1970). Several of the adult females sampled during 1976–1977 in Pyramid Lake exhibited hardened ovaries; concurrent alkalinity levels were in excess of 1,400 mg/l. This condition certainly impairs reproductive success. If the proportion of sexually viable females in the population were decreased in Pyramid Lake by increasing concentrations of alkalinity, the Sacramento perch would eventually be eliminated from the lake.

Sacramento perch from Pyramid Lake usually mature sexually at a mean length of 227 mm. Sexually mature males range in mean length from 160–295 mm, and females at 213–327 mm. Decreasing numbers of male Sacramento perch at larger sizes have been noted by other workers. Mathews (1962) stated that creel census data from Pyramid Lake revealed that about six females per male were taken and that the ratio of older fish was imbalanced in favor of females. In research on Lake Anza, Mathews (1962) also found that all age group V and VI perch were females. Survival of females to older age groups maintains a higher reproductive potential while altering the sex ratios toward the female.

Sacramento perch exhibit high fecundities, as do most members of the family Centrarchidae. During 1976–1977, a sample of 20 female Sacramento perch from Pyramid Lake

TABLE 7. Comparison of mean fecundities of Sacramento perch from Pyramid Lake, 1959-1961 and 1976-1977.

Age ¹ group	n	Mean fecundity		length (mm)	1976-1977
		1959-1961 (Mathews 1962)	Mean n		
II	2	20,825	—	—	—
III	5	62,792	8	295	62,800
IV	5	76,078	9	318	93,279
V	3	112,363	3	327	114,049
VI	—	—	—	—	—

¹Ages from 1976-1977 data assigned by length frequency.

had a mean fecundity of 84,203 eggs. Mathews (1962) reported fecundities, by age group, of Sacramento perch from Pyramid Lake that closely match the 1976 data of corresponding age groups (Table 7). The mean fecundity of 67,672 eggs that Mathews (1962) observed can be attributed to his sample containing a larger proportion of young fish.

A slow-growing population of Sacramento perch from Lake Anza, California, averaged

11,439 eggs per female. Because fecundity is a direct function of fish size, the larger Pyramid Lake fish would be expected to have more eggs. The fecundity of Sacramento perch shows a significant linear relationship with both fork length (mm) and weight (g) ($P < 0.05$) (Fig. 3).

The mature egg diameter for Pyramid Lake Sacramento perch during 1976 varied from 0.79 to 1.00 mm (mean = 0.88). In 1962 Mathews reported that egg diameters of Sacramento perch from both Lake Anza and Pyramid Lake averaged 0.67 mm.

HABITAT AND ECOLOGY

Sacramento perch are currently the least abundant of the five major fish species in Pyramid Lake. A very limited habitat is one reason for the relatively low number of perch. This species is apparently restricted to shallow inshore areas, i.e., the littoral zone. During two years of sampling, almost all Sacramento perch were taken in shore sets.

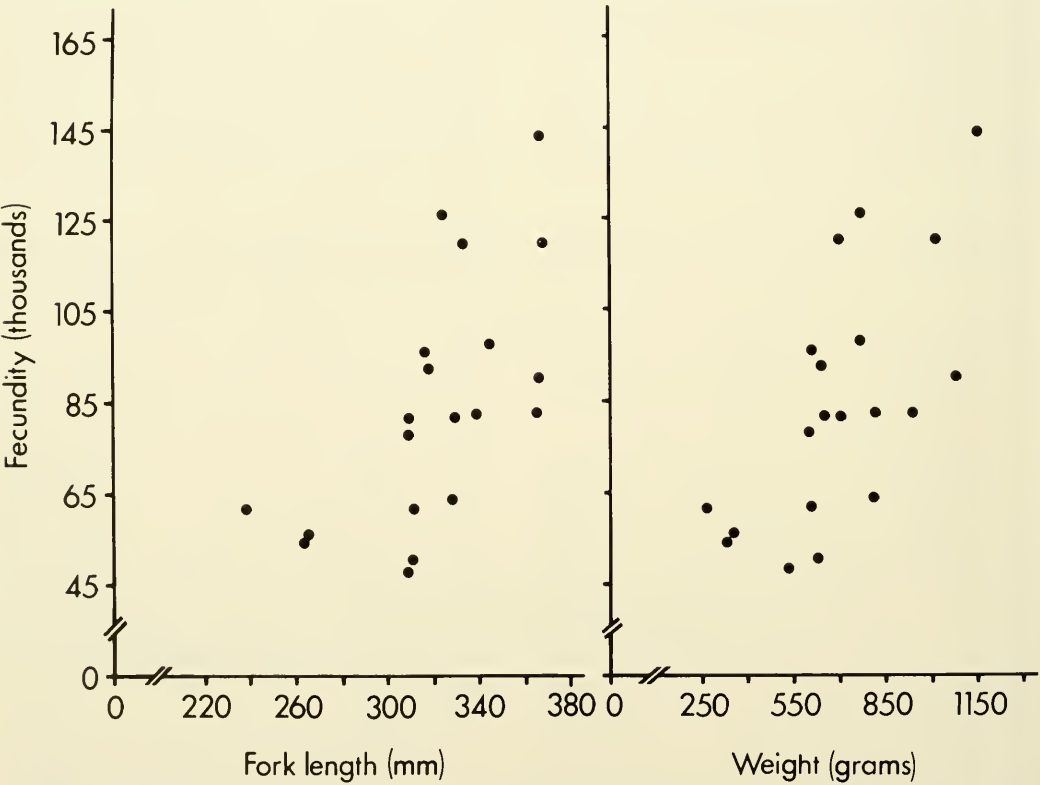


Fig. 3. Length-fecundity and weight-fecundity relationships for 20 Sacramento perch collected in Pyramid Lake, Nevada, during 1976 and 1977.

None were captured at depths greater than 23 m nor in offshore (limnetic) waters at any depth. The littoral zone (0–15 m) of Pyramid Lake provides only about 11 percent of its surface area and about 1.27 percent of the total volume.

LaRivers (1962) notes the sedentary nature of Sacramento perch and their association with rocky habitats and crevices. Recent observations by divers confirm the observation that these fish congregate around rocky points, breakwaters, and tufa caves. Our quantitative net samples indicate that the greatest numbers of Sacramento perch were taken in areas of tufa substrate. The favored habitat of this fish seems to be areas of extensive tufa development, e.g., the Pyramid and vicinity, Hells Kitchen, the Pinnacles, and Pelican Point.

There was no apparent short-term change in abundance of Sacramento perch during 1976 and 1977. The mean catch effort of 177 standardized (18 hr) gill net sets during 1976 (0.29 fish/net) was not significantly different from that of 172 comparable net sets during 1977 (0.33 fish/net) ($P = 0.77$, $F = 0.09$). Due to high within-season variation, no sig-

nificant difference was detected in mean catch of Sacramento perch by season during 1976 ($P > 0.05$). However, a significant seasonal difference was detected for 1977 ($P < 0.001$). The population was relatively inactive from November through April. For both years, about 85 percent of the total annual catch was taken during May–October.

In Pyramid Lake, temperature has the most pronounced environmental effect on Sacramento perch. Monthly mean catch of Sacramento perch was significantly correlated with water temperature ($r = 0.577$, $P < 0.01$). During both years, minimum gill net catches corresponded to temperature minima; catch rate subsequently increased during spring and peaked in July at a temperature of about 21.5 C (Fig. 4). We hypothesize that the temporal thermal regime of Pyramid Lake further tends to restrict the population potential of Sacramento perch because optimum temperatures for active feeding and growth are apparently available for such a short time.

Sacramento perch introduced to Nebraska have been most successful in lakes where other fish populations have been artificially

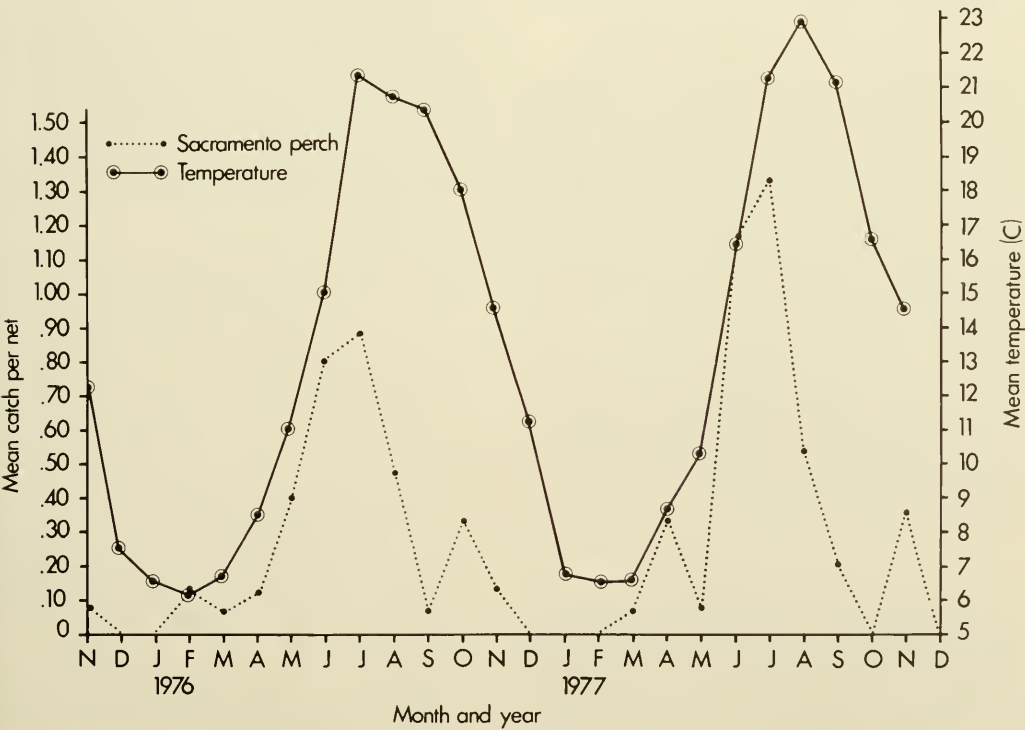


Fig. 4. Mean monthly Pyramid Lake Sacramento perch catches (15 gill net sets per month) from November 1976 through December 1977 in relation to mean surface water temperature.

removed or in highly alkaline lakes that support only a naturally reproducing minnow species (McCarragher and Gregory 1970). Of all waters inhabited by Sacramento perch, Pyramid Lake's environment is most conducive to longevity and maximum growth (Aceituno and Vanicek 1976). The alkaline waters of Pyramid Lake result in a low species diversity. Mathews (1962) attributed the large size attained by Sacramento perch in Pyramid Lake to their highly piscivorous diet. The huge forage base of tui chubs in Pyramid Lake is crucial. Because the alkalinity of Pyramid Lake limits the diversity of its fish species, and the Sacramento perch is the lake's only warm-water piscivore, it holds a stable niche with little interspecific competition.

The fact that the Sacramento perch population apparently did not greatly increase and become a dominant predator when the Pyramid Lake Lahontan cutthroat trout became extinct in the late 1930s indicates that the population does not have a great capacity to increase in numbers and biomass, and that these two game species do not severely compete in Pyramid Lake.

SUMMARY AND CONCLUSIONS

At present, Sacramento perch and Lahontan cutthroat trout are the only species providing a sport fishery in Pyramid Lake. When the Sacramento perch was introduced into Pyramid Lake in the late 1800s, it filled an ecological niche that was previously void. Due to differential spatial and temporal distribution patterns, and the huge production potential of their common food source (tui chubs), the Sacramento perch population does not constitute dangerous competition for Lahontan cutthroat trout in terms of space and energy. Sacramento perch is a unique, relict fish that enjoys the precarious status of a depleted species.

ACKNOWLEDGMENTS

The Pyramid Lake Paiute Indian Tribe was instrumental in initiating the ecological research effort on Pyramid Lake. The Pyramid Lake Ecological study was conducted by W. F. Sigler & Associates, Inc. under contract (#H50C14209487) to the United States

Department of Interior, Bureau of Indian Affairs. Mr. Roy Whaley was responsible for the collection and analysis of the food habits research and Denise Robertson was responsible for age and growth. Dr. William F. Sigler was the directive influence behind the fish life history research on Pyramid Lake.

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BIONOMICS AND CONTROL OF THE WALNUT SPANWORM, *PHIGALIA PLUMOGERARIA* (HULST), ON BITTERBRUSH IN UTAH

Malcolm M. Furniss¹ and Gordon A. Van Epps²

ABSTRACT.— In 1979, the walnut spanworm defoliated a 1 ha bitterbrush seed orchard near Nephi, Utah. No seed was produced for two years thereafter due to feeding damage. Life stages were described and illustrated. The female is brachypterous and incapable of flight. First instar larvae readily drop on their silk threads and probably are dispersed by wind. The insect has one annual generation. Moths laid an average of 159 eggs per cluster in April; larvae began to appear in early May and matured by the first week of June. The pupal period extended from June until mid-April. The parasitic bombyliid, *Villa faustina* (Osten Sacken), was reared from pupae. In April 1980, shrubs contained an estimated average of 1044 eggs each. On 19 May, larvae averaged 1.9 per 7.5 cm of twig and were in the first and second instar. On 20 May the population was controlled by spraying with Sevimol-4. Other potential host plants, as determined from greenhouse tests, are rose, ceanothus, mountain mahogany, serviceberry, and willow.

The walnut spanworm, *Phigalia plumogeraria* (Hulst) was discovered defoliating bitterbrush (*Purshia tridentata* [Pursh] D.C.) in a seed orchard near Nephi, Utah, in June 1979. The larvae had been recorded previously (Rindge 1975) on *Juglans*, *Salix*, *Quercus*, *Malus*, *Prunus*, and *Acer* but not on bitterbrush. The moth is found in British Columbia and most western states. Because of the severity of defoliation and the importance of bitterbrush as big-game browse, we compiled the information reported here.

The best accounts of *P. plumogeraria* (= *Boarmia*) are those of Coquillett (1893, 1894, 1897) in California on English walnut. Rindge (1975) placed *plumogeraria* in the genus *Phigalia* with three other species, of which only the life history of *P. titea* (Cramer) seems to have been studied (Talerico 1968). Rindge's revision includes most of the significant information on *plumogeraria* except the description of the egg and five larval stages by Dyar (1903) and of all stages by McGuffin (1977). Although, as mentioned by Rindge (1975), Hulst evidently intended to name the species *plumigeraria*, we use *plumogeraria* in conformity with Fletcher's (1979) Catalog of Geometroidea.

SEED ORCHARD AND INFESTATION

The infestation occurred 8 km south of Nephi, Juab County, Utah, at 1707 m elevation. Other known adult specimens from Utah were collected at Ogden 23 March 1977.³ Rindge (1975) shows two Utah collections in the vicinity of that reported here.

The 1 ha bitterbrush seed orchard south of Nephi was seeded in 1966 in rows varying from 1.2 to 3.7 m apart. Source of seeds was Fountain Green Divide, approximately 17 km east of Nephi. Plants were thinned from 0.6 to 2.4 m apart within rows to determine optimum spacing. The plants averaged about 1.6 m tall in 1979. The seed orchard is surrounded by grain fields, and the nearest native bitterbrush is more than 3 km eastward.

The top 16 cm of soil consists of a friable reddish brown loam of moderately granular structure. It is mildly calcareous and mildly alkaline. The terrain has a 2 percent slope. Annual precipitation averages 32 cm, with an average of 2.2 cm monthly during June through November and 3.0 cm monthly thereafter. Prevailing winds are from the south or north.

On 17 May 1979, the bitterbrush appeared normal (Fig. 1A) although some small loopers

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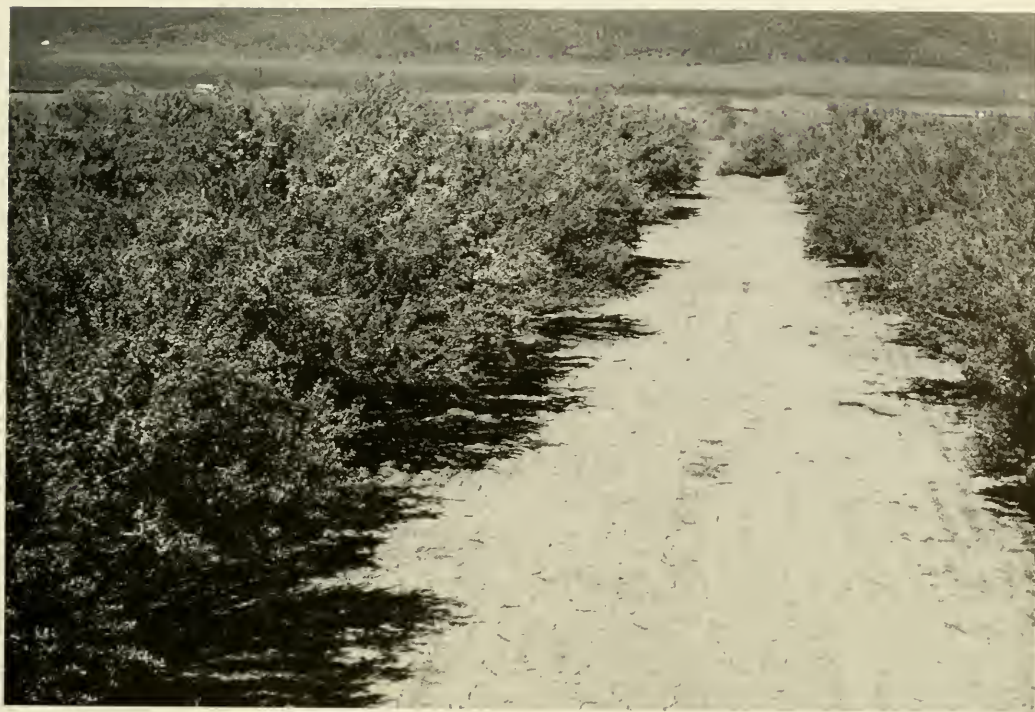


Fig. 1. Bitterbrush shrubs on 22 May 1979 before defoliation (A), and 6 June after defoliation (B) by walnut spanworm.

TABLE 1. Head widths of *Phigalia plumogeraria* larvae reared in greenhouse from eggs collected 10 April 1980.

Instar	No. of larvae	Head width (mm)	
		Average	Range
1	30	0.40 (0.39) ¹	0.37–0.43
2	30	0.70 (0.67)	0.68–0.78
3	30	1.15	1.09–1.21
4	30	1.78	1.69–1.89
5	30	2.62 (2.71)	2.54–2.87

¹Figures in parentheses are averages from field populations; first and second instar larvae collected between 3–20 May 1980, fifth instar larvae collected 6 June 1979.

were present as recalled later. Plants had bloomed fully 22 May, with many more flowers than in previous years, and a good seed crop was expected.

During our next visit 6 June we found the orchard completely defoliated (Fig. 1B) and devoid of developing fruits, except on a few border plants. Mature larvae were collected and sent to the USDA Systematic Entomology Laboratory, Beltsville, Maryland, but could not be identified. We therefore set about rearing all life stages, taking photos, and developing information that would enable identifying and controlling the insect should it be encountered in the future.

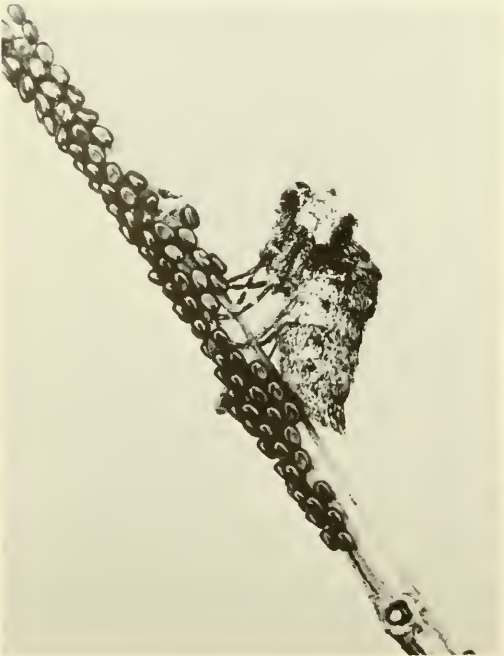


Fig. 2. Female moth and eggs on bitterbrush twig.

LIFE STAGES

Egg

The 0.89 × 0.67 mm oval-shaped egg (Fig. 2) is slightly blunted at the micropyle end and is flattened on two sides. Coquillett (1893) described the color as dark grayish drab with a strong brassy tinge, although it reminds us of pewter. At low magnification, the chorion is slightly wrinkled transversely, except at the ends, which appear to have been dented with a ball peen hammer.

Larva

The larva is of the usual geometrid type (Fig. 3) and has five instars, during which it varies in body length from 2 or 3 mm to as much as 34 mm. Head widths of larvae are shown in Table 1. The crochets of mature larvae form a biordinal mesoserries.

FIRST INSTAR.—Length 2 to 3 mm, appearing blackish to the unaided eye, but under magnification the body is mottled dark brown with a broken white lateral line. The head is uniformly black and smoothly



Fig. 3. Mature larva on bitterbrush.

rounded; the abdomen lacks prominent tubercles that are present in subsequent instars.

SECOND INSTAR.—Length 5 to 6 mm, appearing blackish brown to the unaided eye, but under magnification the body segments are blackish with lighter intersegmental areas. The head is mottled brownish and has fairly prominent, rounded epicranial lobes as in all subsequent instars. Primary setae are supported by prominent, darkly pigmented tubercles on several abdominal segments. Using Hinton's (1946) classification, the relative size of the most prominent dorsal tubercles is $D2 > D1$ on the first four abdominal segments (A1–4), but $D1 > D2$ on abdominal segment 8 (A8). The tubercle supporting seta L1 posterior of the spiracles is also prominent, particularly on A1–4. The relative size of the previously mentioned tubercles is $A2$ and $A8 > A1 > A4$.

THIRD INSTAR.—Length 10 to 12 mm, color yellowish brown with contrasting black tubercles. Otherwise as described for second instar.

FOURTH INSTAR.—Length 14 to 21 mm, color variable: greyish cream, sometimes with a pinkish cast to body and head capsule.



Fig. 4. Male pupa, ventral view.

Otherwise as described for previous two instars.

FIFTH INSTAR.—Length 18 to 35 mm, color greyish or greyish yellow in the field population, sometimes with a pinkish cast in reared larvae. Tubercles as described for instars 2 through 4 except their tips are orangish or yellowish brown, and the setae tend to be longer than their supporting tubercles rather than equal or shorter, as in earlier instars.

Pupa

The pupa (Fig. 4) is rather stout and shiny dark brown. It varies in length from 10 to 15 mm.

Females are generally wider and shorter than males:

	Female	Male
Length, mm	11.7	12.8
Width, mm	4.3	4.2
Ratio W/L	0.37	0.33

A two-spined cremaster is located at the tip of the abdomen. In some species a short projection occurs on each side at the base of the cremaster, but these are usually not of sufficient shape or length to be described as spines. Field-collected pupae often have tips of the cremaster spines broken.

As seems general in Lepidoptera, the genital opening of the female is located between abdominal segments 7 and 8, and that of the male spans segment 8. The impression of the antennae is similar in both sexes, but the edges are more elevated in the male. The best characteristics for separating the sexes of *plumogeraria* are the wings and side profile. The female's wings are vestigial, and she appears more hunchbacked than the male (Fig. 5).

Adult

The adult (Figs. 2 and 6) is described in detail by Rindge (1975). The characterization presented here will permit definitive separation of *P. plumogeraria* from other geometrids infesting bitterbrush. For example, the female of *Anacamptodes clivinaria profanata* (Barnes and McDunnough) is winged (Furniss and Barr 1967); wings of female *P. plumogeraria* are functionless minute pads. Likewise,

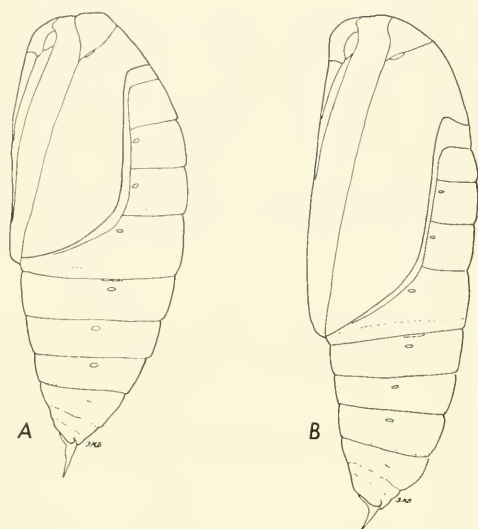


Fig. 5. Left side perspective of female (A) and male (B) pupa.



Fig. 6. Male moth on bitterbrush.

males are separable merely by the very broadly bipectinate antennae of *P. plumogeraria*.

MALE.— Body 10 to 11 mm long, brownish grey. Wings large, grey color; forewing 18 to 24 mm, sometimes weakly marked with two dark cross lines. Antennae bipectinate with long (0.5–2.8 mm) biciliate pectinations, from which the specific name aptly derives. Dorsum of abdomen reddish brown.

FEMALE.— Body 7 to 11 mm; head, thorax, and appendages grey. Antennae simple. Dorsum of first abdominal segment covered by a dense mat of black spines and scales; remaining segments with reddish brown scales trailed by mixed black and white spines or scales; whitish underneath abdomen.

SEASONAL HISTORY AND BEHAVIOR

In California, moths were reported to emerge between early January and late March (Coquillett 1897). Larvae matured there in the latter part of April and pupated in soil during May. One generation occurred annually. In Utah, however, those events occurred later in the bitterbrush orchard, probably due to the colder climate.

Adult

In the orchard, moths were abundant 7 April 1980 and are presumed to have begun emerging several days earlier. (Time of emergence could be inferred also from five males caught in flight at Ogden, Utah, 23 March 1977.⁴ Mating was not observed. The duration of adult presence was not determined, but females seemed to outlast males.

Egg

Eggs were first observed 7 April 1980, while bitterbrush was still dormant. Eggs were laid only on 1979 terminals, mainly in the upper crown, on their flat side in closely spaced masses of 23 to 345 eggs (average 159). Of egg masses sampled, 23 percent had been laid in 1979; 77 percent were laid in 1980, but we don't know if this represents the relative size of those generations.

Eggs were very abundant when collected for incubation 12 April. Hatching began in the field before 2 May and was virtually

⁴Ibid.

complete on 16 May. Eggs incubated at 22–24 C hatched in 10 days. Larvae emerged from the micropyle end. Examination of 22 incubated egg masses disclosed that 17 percent of the eggs were not viable.

Larva

Larvae were first observed 2 May. Newly hatched larvae dropped readily on silk threads after encountering the end of a twig or edge of a leaf. This behavior aided their dispersal by wind. Later instars dropped on threads only when touched or jarred.

Larvae were sampled in 1980 prior to application of insecticide on 20 May. The proportion of instars by date were:

Date	Number	Instar I	Instar II
		(Percent)	
8 May	48	100	
13 May	71	99	1
16 May	56	66	34
19 May	123	58	42
20 May	303	8	92

No further observations were possible because of elimination of larvae by treatment we will discuss later. In 1979, however, larvae had matured by 6 June. Such rapid development of the ravenous later instars accounts for the sudden defoliation in 1979 (no damage visible 22 May; completely defoliated before 6 June). Likewise, Coquillett (1893) quoted a Santa Barbara walnut grower who saw his orchard eaten up in the space of one week.

Larvae were reared at 21 C, 17 hr day. The duration of instars was as follows:

Instar	Number	Duration (days)	
		Average	Range
I	30	4.5	4–5
II	30	2.5	1–4
III	28	3	1–6
IV	23	4	2–6
V	17	11	9–13
Total		25	17–33

The duration of fifth instar larvae may have been prolonged by depletion of foliage periodically, due to their capacity to consume leaves. Four host plants were infested to compare their suitability to larval growth. Larvae grew fastest on wild rose (*Rosa* sp.) and redstem ceanothus (*Ceanothus sanguineus* Pursh.), followed by mountain mahogany (*Cercocarpus ledifolius* Nutt.), then

bitterbrush. Possibly the reason for slower development on bitterbrush was that smaller leaves of that plant may have resulted in larvae intermittently running out of food before being transferred to other plants. In the greenhouse, some larvae wandered onto potted Scouler's willow (*Salix scouleriana* Barratt) and serviceberry (*Amelanchier alnifolia* Nutt.) and appeared to feed and develop normally.

Pupa

Date of pupation was not determined precisely but probably occurred in 1979 soon after 6 June, when all larvae were in their fifth instar and foliage had been eaten. Pupae are known to have been in the soil 10 July, but no observation was made between those dates. Diapause was present in pupae and was broken with only fair success by refrigeration for over 90 days at ca 2 C followed by rearing at room temperature.

In 1980, termination of the pupal stage in the field obviously began prior to 7 April, when adults and eggs were seen on plants. Some pupae were found in soil 12 April, but most moths are believed to have emerged by then. Pupae occurred in the upper 10 cm of soil and were more abundant closer to the base of the plant.

POPULATION SAMPLING

On 10 and 11 April 1980, we collected one egg mass from 1979 terminals of three shrubs from every other row. The sample shrubs were located near the ends and middle of each row. The egg mass chosen was the third one encountered from an arbitrary beginning point. A total of 33 egg masses were obtained; 26 had current-year eggs and 7 had empty 1979 eggs. The 1980 egg masses had an average of 159 eggs (SD = 71.8). Examination of the 33 sample shrubs disclosed 261 egg masses (average/shrub = 7.91, SD = 5.35).

The 1980 population of eggs in the entire orchard is estimated to have been: 407 shrubs × 7.91 egg masses × 159 eggs = 511,880. If 83 percent were viable, as indicated by incubation of a sample lot, the orchard contained 424,860 first instar larvae, or 1,044 larvae

per shrub. On 20 May, after insecticide was applied, 500 second instar larvae were collected on a sheet beneath one shrub; thus, allowing for dispersal and natural mortality, the estimate of initial larval population may be accurate.

On 19 May, a 7.5 cm twig was taken from the north and south sides of each of the same 33 shrubs from which eggs had been sampled 10 and 11 April. As noted earlier, 58 percent of the larvae were first instar; 42 percent were second instar. Results were:

	North	South	Both
Total larvae	53	73	126
Aver. no./7.5 cm	1.61	2.21	1.91
SD	1.46	1.60	1.55

Only 10 of the 66 twigs had no larvae; range was 0 to 7 larvae.

CONTROL

Natural Control

Coquillett (1897) reported two larval parasites: an unidentified tachinid and an undetermined species of *Apanteles* (Ichneumonidae). Our search of parasite records has disclosed no additional information, although *P. titea*, which occurs generally more eastward, has six parasites (Talerico 1968).

We discovered one parasite, a bombyliid fly, *Villa faustina* (Osten Sacken), which emerged in early June from *P. plumogeraria* pupae collected from soil in early April 1980. It was not abundant enough to be a significant control factor. We also commonly found wings of males in early April that we think resulted from predation by birds. Coquillett (1897) noted that blackbirds preyed on larvae in California.

Soil characteristics and the inability of females to fly also affect abundance of *P. plumogeraria*. Soil that is friable is well suited for larvae to enter and pupate. Compact soil is less suited to pupation because its density presents a physical barrier and is more apt to heat to a temperature harmful to larvae seeking to pupate.

The inability of female moths to fly limits their dispersal. Probably adult females and immature stages are occasionally transported accidentally by man's conveyances. But, judging from observations of larval behavior, dispersal apparently occurs mainly by wind after eclosion of larvae.

Applied Control

Prior to April, sticky barriers could be applied to stems to prevent female moths from climbing the plants to oviposit. This method may be feasible in a seed orchard but not over an extensive area.

Larvae in the first and second instars were controlled effectively by treatment 20 May 1980, with a spray consisting of 2.93 ml Sevimol-4⁵ per liter of water. Sevimol-4 contains 40 percent carbaryl. The spray was applied in calm air at the rate of 593 l/ha with a modified John Deere garden sprayer⁶ pulled behind a 14 hp John Deere garden tractor. A broad jet with adjustable nozzles was mounted on a pipe approximately 1.8 m behind the sprayer. The jets were adjusted to deliver spray outward. The tractor was driven up every other row. Whereas the prespray population (19 May) was 1.91 larvae per 7.5 cm of twig, only 5 live larvae were found on 30 plants 22 May.

DISCUSSION

Occurrence of this outbreak on bitterbrush carries some lessons. Even a well-studied shrub may be seriously damaged by native insects not previously known on that shrub. Examples of similar geometrids killing mountain mahogany for the first known time are *Anacamptodes clivinaria profanata* (Barnes and McDunnough) in southwestern Idaho (Furniss and Barr 1967) and *Stamnodes animata* (Pearsall) in northwestern Nevada (Furniss et al. in preparation). Both of those insects were unstudied and difficult to identify. Information such as host plants, biology, and immature stages was lacking until the insects' sudden destructiveness attracted study. Along with potential damage by such native insects,

⁵Although this paper reports research involving a pesticide, it does not contain recommendations for its use nor does it imply that the use discussed has been registered. All uses of pesticides must be registered by appropriate state and/or federal agencies before they can be recommended.

⁶The use of trade, firm, or corporation names in this report is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

there is an ever-present possibility of introduction of new insects as well as diseases (Furniss and Krebill 1972).

Results of our study will alert others to the potential of this geometrid to infest shrubs of several species. Besides feeding on bitterbrush in the field, in the greenhouse the larvae fed and matured on rose, redstem ceanothus, curleaf mountain mahogany, saskatoon serviceberry, and scouler's willow.

Should other infestations occur, the insect can now be readily identified in all its stages. Information needed for control is available, including seasonal history, behavior, criteria for determining instars, and a method of treatment of high value shrubs such as in a seed orchard. We regret, however, that we couldn't observe an unaltered outbreak to determine long-term effects. Only then could we determine whether or when an outbreak in a natural shrub stand would require control or how to control it.

ACKNOWLEDGMENTS

Moths were identified by Dr. Douglas C. Ferguson, Lepidoptera Section, USDA Systematic Entomology Laboratory, Washington, D.C. The bombyliid was identified by Dr. Jack Hall, Division of Biological Control, University of California, Riverside. We were assisted in the field by Eric Christensen, Utah State University, and Blaine Moore, Snow College, Ephraim, Utah. Charles R. Hepner, Jeffrey Littlefield, and Frances M. Bales, USDA Forest Service, Moscow, Idaho, assisted with rearing and measuring specimens. Frances also drew Figure 5. The manuscript was reviewed by Dr. William F. Barr, Department of Entomology, University of Idaho; Dr. Arthur R. Tiedemann, USDA Forest Service, Provo, Utah; and Charles F.

Tiernan, USDA Forest Service, Missoula, Montana.

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BIRD COMMUNITY COMPOSITION IN RELATION TO HABITAT AND SEASON IN BETATAKIN CANYON, NAVAJO NATIONAL MONUMENT, ARIZONA¹

Jack D. Brotherson², Lee A. Szyska², and William E. Evenson³

ABSTRACT.— Bird species density, diversity, and species richness in relation to habitat and seasonal variations were studied in the Betatakin Canyon area of Navajo National Monument, Arizona. The two most prominent habitat types are a riparian forest deep in the canyon bottom and a mature pinyon-juniper woodland on the mesas and slopes above the canyon. One hundred thirty-five species of birds were encountered during the study and recorded by season and habitat. The avifauna assemblages demonstrate definite habitat selection into groups associated with the riparian and pinyon-juniper woodland communities. Diversity, density, and species richness were greatest in the riparian habitat during the spring and summer months. The differences in bird community composition were greater between seasons than between habitats. Pinyon pine and Gambel oak were highly selected as perch sites in the pinyon-juniper and riparian areas, respectively.

As part of an ongoing ecological survey of Navajo National Monument, we studied the bird communities and report here their ecological relationships with respect to vegetation and season.

The effects of habitat diversity and seasonal change on bird species diversity have been extensively documented in ecological literature (MacArthur and MacArthur 1961, Karr and Roth 1971, Willson 1974, Karr 1976, Roth 1977, Balda and Masters 1980). Two of the most commonly investigated components of habitat diversity are foliage height and plant species composition (MacArthur and MacArthur 1961). Willson (1974) demonstrated that as forest canopy becomes increasingly stratified, additional foraging guilds (bird groups of similar foraging habitat and behavior) are able to invade, thus increasing species diversity. The inter-relationship between species diversity, foliage height, and vegetational complexity has been explored by a number of researchers (Johnston and Odum 1956, Johnsgard and Rickard 1957, Karr 1968, Cody 1974, Yeaton 1974, Whitmore 1975 and 1977, Johnson 1975).

In more complex habitats, however, foliage height diversity alone is not a reliable predictor of species diversity. MacArthur and MacArthur (1961) suggested that birds living

in desert scrub might require more than foliage height differences to partition their environment. This was subsequently confirmed by Tomoff (1974), who found that plant species composition was the best determinant of bird species diversity in desert scrublands. He suggested that the extreme diversity in growth forms of desert plants would provide greater habitat variability than would differences in mature plant height.

STUDY SITE

Navajo National Monument is in northeastern Arizona about 16 km northwest of Black Mesa and Arizona Highway 160. The principle sites of the monument are three large Anasazi Indian cliff dwellings located in three separate canyons. Betatakin Canyon belongs to the Tsegi Canyon complex, which has been described by several authors (Gregory 1916 and 1917, Hack 1942 and 1945, Harshbarger et al. 1957, Cooley 1958, 1962, Woodbury 1963).

The major geological formation within Betatakin Canyon is the Navajo Sandstone, which forms sheer cliffs towering more than 200 m above the canyon floor. The floor itself, at an altitude of about 2100 m, consists of deep alluvial deposits of sandy Quaternary fill, overlain by talus at the base of the cliffs.

¹Completed as part of Contract PX7029-8-0570 from the Southwest Region of the National Park Service.

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The Kayenta Sandstone formation outcrops beneath the Navajo and is occasionally seen in the lower reaches of the canyon.

The annual temperature recorded at Park headquarters within the Monument ranges from -23 to 38 C, with a mean of 10 C. The number of frost-free days during the year varies from 107 to 213, with an average of 155 days. Total annual precipitation in Betatakin has historically ranged from 17 cm to 48 cm, with a yearly mean of 29 cm. There is a single wet season, lasting from late summer to early fall. Rainfall within the canyon is variable and spotty, with localized cloudbursts rather than large regional storms.

A mature pinyon-juniper community occurs on the mesa and slopes above the canyon and extends onto the exposed slickrock and walls that slope down to the canyon floor. Although pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) are consistently the dominant overstory species, there are 3 distinctive understory communities (Brotherson et al. 1980) dominated by big sagebrush (*Artemisia tridentata*), littleleaf mountain mahogany (*Cercocarpus intricatus*), and a mixed shrub zone consisting of cliffrose (*Cowania mexicana*), antelope bitterbrush (*Purshia tridentata*), cliff fendlerbush (*Fendlera rupicola*), and roundleaf buffaloberry (*Shepherdia rotundifolia*).

A riparian forest and associated trees grow on the canyon floor and along the talus banks above the intermittently flowing stream. Many of the plant species found here are usually associated with high mountain habitats. The dominant species include quaking aspen (*Populus tremuloides*), box elder (*Acer negundo*), water birch (*Betula occidentalis*), redbarked dogwood (*Cornus stolonifera*), Gambel oak (*Quercus gambelii*) and Douglas fir (*Pseudotsuga menziesii*).

METHODS

Birds were censused during all four seasons of the year by the transect method (Emlen 1971 and 1977) on 7-10 May, 8-10 July, 6-7 November 1978 and 19-21 February 1979. Three transects, each one-half mile in length, were established as follows: one in the canyon bottom, one in the pinyon-juniper-mixed shrub community type, and one in the

pinyon-juniper sage community type. Censusing was done in early morning and evening on three consecutive days each season. During a separate spring and summer census from May through August of 1977, five Emlen transects were run twice a month, and the perching site of each bird seen was also recorded. Birds observed flying through the area were not included in the analyses, although such sightings are included in the species list for the monument.

Types of habitat were distinguished on the basis of vegetational differences (Brotherson et al. 1980). Standard diversity indices (H' , J') were calculated for the bird assemblages seasonally and within the different habitats (Pielou 1975). The diversity of a community depends on two variables: (1) number of species present and (2) evenness with which the individuals of the species are scattered through the community (Kricher 1972). To describe a community's diversity only in terms of its diversity index (H') is to confound these two factors. A community with a few, evenly represented species can have the same diversity index as one with many, unevenly represented species. Therefore, we also calculated the equitability index, (J') that is designed to measure this evenness component (Lloyd and Ghelardi 1964). (See May 1975 for a review of diversity indices and their applicability.)

Niche width and niche overlap values (Colwell and Futuyma 1971) were also calculated. Niche width is a measure of the breadth of use of the available resources (in this study, habitat types and seasons). Niche overlap measures the amount of mutual utilization of resources by two species.

Birds were clustered, using unweighted pair group averages, on niche overlap (Sneath and Sokal 1963), using as resource bases habitat type, individual perch site, and seasonal occurrence. Additional cluster analyses were run to check the effects of seasonality and habitat, using Ruzicka's (1958) similarity index, without respect to niche overlap.

RESULTS

One hundred thirty-five species of birds are known from Navajo National Monument

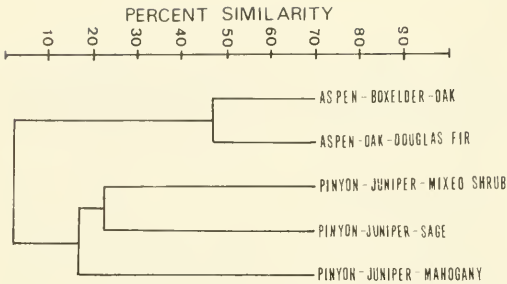


Fig. 1. Dendrogram of the cluster analysis of bird habitat information taken in the spring and summer of 1977 using Emlen transects.

(Appendix). Sixty-six species were noted in Betatakin Canyon during the 1978–1979 census, and 43 during the spring 1977 census. Of these 43, 10 were eliminated from our analyses because they were only sighted once.

The avifauna assemblages demonstrate definite habitat selection. A clustering of the data from the spring and summer census of 1977 (Fig. 1) shows a clear separation of the bird fauna associated with the riparian and pinyon-juniper communities (2 percent similarity). Subzones of the riparian communities are distinguished as streambank habitats (aspen, box elder, and some Gambel oak) and talus slope habitats above the stream (aspen, Gambel oak, and Douglas fir). The subzones of the pinyon-juniper communities are distinguished by their principle understory species (sagebrush, mountain mahogany, and mixed shrubs). Later analyses lumped the subzones of the riparian community into one. Those of the pinyon-juniper community were lumped into two by combining the P-J mahogany subzone with the P-J mixed shrub subzone because these two P-J subzones are floristically almost indistinguishable (Brotherson et al. 1980).

The riparian and pinyon-juniper communities support highly distinct avifauna. The riparian habitat supports nearly a third more species than the pinyon-juniper habitat (Table 1). The total density of individuals in the riparian communities is about 60 percent greater than the mixed shrub zone. The number of species seems to be the major factor determining diversity in the avian community rather than the relative abundances of the species present.

Avian niche widths are similar during the spring and summer. Average niche overlap

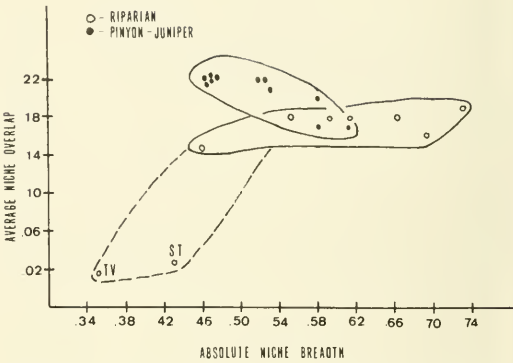


Fig. 2. Graph of average niche overlap values against absolute niche width values from data taken in summer. Depicts only riparian species and pinyon-juniper species restricted to those zones.

(mean of all niche overlaps between a given species and all other species) against absolute niche width is shown in Figure 2. Only those birds found exclusively in either the pinyon-juniper or riparian habitats were included. Exclusion of the two outlying points (Turkey vulture and Swainson's thrush, which were observed only in the Douglas fir and on the ground), suggest that habitat use, as deduced from the niche metrics, is similar in the two communities (Fig. 2).

Habitat use patterns change through the year. The pinyon-juniper-sage and mixed-shrub zones remain similar, as expected, but riparian habitat use becomes much broader (Fig. 3). Early spring migrants arriving before the riparian forest has leafed out face limited resources and are therefore forced to forage widely. The deciduous nature of the forest also precludes specialization during the winter months when food resources become scarce.

TABLE 1. Major habitat types along with their total number of bird species, total densities (D) and diversities (H', J').

Community type	No. of avian species	D	H'	J'
Riparian	46	17.4	1.455	.380
Pinyon-Juniper-Sage	34	15.4	1.301	.389
Pinyon-Juniper-Mixed shrub	36	10.8	1.307	.305

D = Total densities of all individuals present per ha
H' = Shannon-Weaver Diversity index = $\sum p_i \log p_i$, where p_i equals the proportion of a species in the whole community.
J' = Equitability index = $H' / \log S$ where S = total number of species present in habitat.

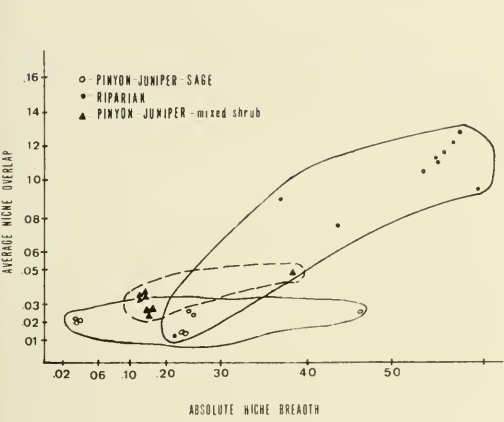


Fig. 3. Graph of average niche overlap values against absolute niche width values from data taken throughout the year. Depicts values for birds restricted to any one of the three habitat types sampled: riparian, pinyon-juniper, and pinyon-juniper-mixed shrub.

Perch Site Selection

The spring-summer census of 1977, which recorded specific perch sites, permits examination of tree use within and between habitats. We identified the nine most frequently chosen perches (those plant species with less than three sightings were excluded from analysis) and calculated diversity indices (Table 2). Excluding the ground category, which is common to both communities, riparian habitat has 26 percent more bird species than pinyon-juniper, but the largest numbers of birds are found in pinyon pine and oak. The use of pinyon pine and oak is not simply a function of availability, because cover of mature pinyon pines and junipers is approximately equal in the P-J community, and cover of Gambel oak and aspen is approximately

TABLE 2. Perching sites of birds from the spring-summer census of 1977. N = total number of individuals, H' = Shannon-Weaver diversity index, J' = equitability (see Table 1).

Perching sites	No. of species	N	H'	J'
Aspen°	11	42	.910	.379
Box elder°	9	43	.855	.389
Gambel oak°	19	137	1.037	.352
Douglas fir°	10	49	.555	.241
Dogwood°	4	6	.578	.417
Pinyon	23	149	1.025	.327
Juniper	12	24	.994	.400
Mahogany	7	58	.366	.188
Ground	5	28	.513	.319

°R = Riparian community
P-J = Pinyon-juniper community

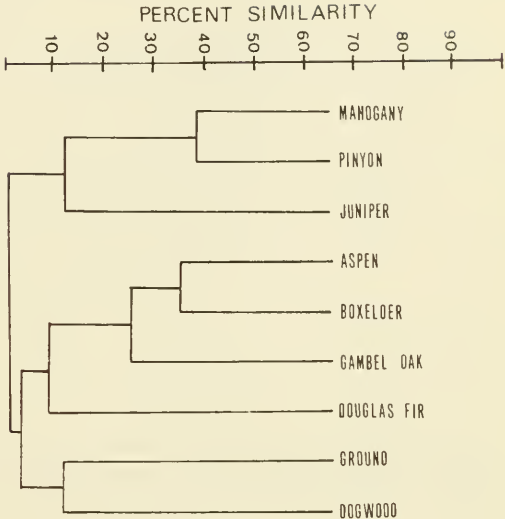


Fig. 4. Dendrogram of the cluster analysis of perch site choice of bird species (summer 1977 data only).

equal in the riparian community. Furthermore, box elder also makes a substantial contribution to cover in the riparian community. The disproportionate use of pinyon and oak is reflected in the high H' values and the lower J' values, suggesting that these tree species are used preferentially by many species throughout the spring and summer. This unequal use of pinyon pine and oak is possibly due to greater availability of insects associated with these trees (Balda 1969) than with neighboring juniper or aspen (S. L. Wood, pers. comm.). In addition, greater foliage density in oak than in aspen may attract some birds.

Cluster analysis applied to the perching data taken in the 1977 census (Fig. 4) exhibits general patterns similar to those shown in Figure 1 and confirms the distinction between bird communities in the riparian and pinyon-juniper habitats. It also permits separation of the subzones within these communities by their bird species components. Figure 5 shows a cluster by niche overlap of 33 bird species associated with the recorded perch sites. The cluster identified 9 major groups (for species identification within each group, see Table 3).

Seasonality

Numbers of both species and individuals increase during the spring and summer, with

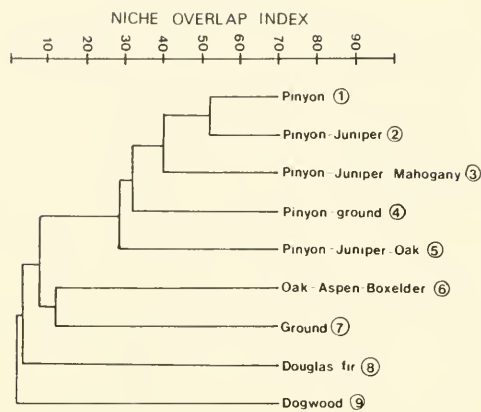


Fig. 5. Dendrogram of the cluster analysis of 33 bird species by niche overlap from perch site data. For identification of bird species found in each group see Table 3.

correspondingly high diversity values (Table 4). The avifaunal similarities are greater in all habitat types in spring-summer versus the fall-winter component in the same habitat (13 percent similarity, Fig. 6). Nevertheless, the riparian fauna is clearly distinct from the pinyon-juniper-sage and pinyon-juniper-mixed shrub fauna in both the spring-summer and fall-winter seasons (Fig. 7). The two pinyon-juniper subzones are distinguished only during the fall and winter months, become less so in spring, and show high similarity (56 percent) during the summer.

TABLE 3. Bird species grouped by cluster analysis of niche overlaps (date from perch site information). Table corresponds to Figure 4.

Group	Species	Group	Species
1	Mourning Dove Violet-green Swallow Brown-headed Cowbird Bluebird Bushtit	6	Virginia's Warbler Sharp-shinned Hawk Audubon's Warbler Black-headed Grosbeak Hairy Woodpecker Dusky Flycatcher Warbling Vireo Downy Woodpecker Ruby-crowned Kinglet White-breasted Nuthatch Hermit Thrush Flicker
2	Black-throated Gray Warbler Rock Wren Gray Flycatcher Plain Titmouse	7	Rufous-sided Towhee Swainson's Thrush
3	Chipping Sparrow Common Bushtit	8	Black-capped Chickadee Turkey Vulture
4	Gray-headed Junco	9	Wilson's Warbler
5	Black-chinned Hummingbird Scrub Jay Blue-gray Gnatcatcher Mountain Chickadee		

A clustering of all 66 bird species according to season identifies six major groups corresponding to summer resident, winter resident, and permanent resident categories, as well as migrants in the appropriate season (Fig. 8).

Habitat Preference and Niche Overlap

Niche overlaps of all 66 species are represented by a cluster diagram (Fig. 9). The birds were clustered according to both season and habitat. The clustering identifies 13 major groups (For species identifications within each group, see Table 6). Birds restricted to the pinyon-juniper-sage and pinyon-juniper-mixed shrub habitats (habitats with the least apparent floristic diversity), and those found in the canyon during the harsh winter months show the narrowest niches and the least overlap with other species. Those found in the riparian forest or during the spring and summer months have broader niches and show considerably greater niche overlaps (Figs. 2, 3, and 10). Our data do not permit us to differentiate between birds that are better adapted to harsher, resource-poor habitats and those that are competitively excluded from other areas and subsisting on the extreme edge of their habitat tolerance. In other words, we cannot clearly separate local seasonal exclusions from habitat selectivity (Rosenzweig 1975).

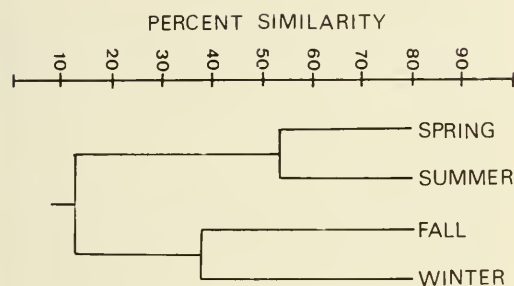


Fig. 6. Dendrogram of the cluster analysis of data on bird communities by season.

DISCUSSION

Bird species diversity in Betatakin Canyon follows plant species diversity, with different avifaunal assemblages occurring in the deciduous riparian and evergreen scrub communities. The birds of Betatakin are not randomly distributed through the canyon, but are specific to habitat and season. Habitat selectivity has long been known to occur between successional stages of forests, with entire suits of fauna replacing one another as a forest succeeds toward the climax stage (Johnston and Odum 1956, Johnsgard and Rickard 1957).

Tomoff (1974) demonstrated that plant species diversity and lifeform were the best predictors of bird species diversity in desert scrubland. Our data support this hypothesis; plant species diversities were 4.6 in the riparian community and 2.3–2.6 in the two P-J zones. The data also suggest that the full range of plant species diversity in Betatakin is required to maintain the high diversity of bird species found there. This implies that species diversity may be tied to availability of niches (Rosenzweig 1975).

There are some theoretical anomalies worth considering because they point out

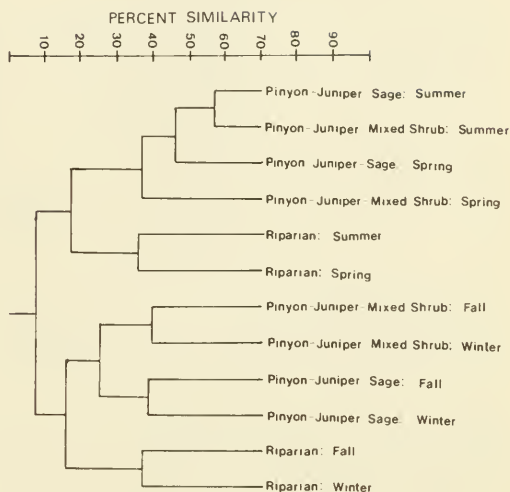


Fig. 7. Dendrogram of the cluster analysis of data on bird communities by habitat and by season.

factors peculiar to the canyon. Assuming that resource availability peaks in the spring and summer, and if abundant resources permit extensive resource partitioning, then both niche width and niche overlap should be smallest in the spring and summer (Fig. 10). The reverse is occurring, however, and several factors may help to explain this. First, during the late fall and winter, the available food resources become localized in the dried fruits and seeds of the riparian forest and in the limited remaining evergreen community. Regardless of abundance, this narrow resource spectrum automatically generates mathematically small niche widths, although one might expect niche overlap to be greater than observed. The small niche overlap values obtained may be a result of the species pool dropping from 45 in the summer to 12 in the winter, a loss of almost 75 percent. Resource partitioning may have occurred

TABLE 4. Summary of population data collected on census in the Betatakin Canyon area of Navajo National Monument.

Habitat type	Number of species				Mean density*				Shannon-Weaver (H')			
	Sp	S	F	W	Sp	S	F	W	Sp	S	F	W
Riparian	34	26	7	5	5.7	7.0	1.9	1.6	1.71	1.19	0.83	0.34
Pinyon-Juniper mixed shrub	24	27	5	7	3.8	4.9	1.5	0.7	0.87	1.38	0.56	0.57
Pinyon-Juniper-Sage	22	24	9	9	5.4	3.6	3.7	2.7	1.14	1.23	0.68	0.82

Sp = Spring. Census period: 7–10 May

S = Summer. Census period: 8–11 July

F = Fall. Census period: 6–7 November

W = Winter. Census period: 19–21 February

*Individual birds per ha.

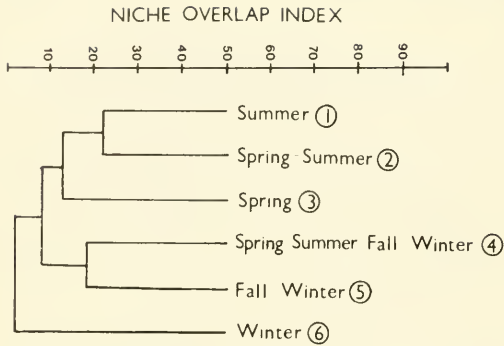


Fig. 8. Dendrogram of the cluster analysis of 66 bird species by niche overlap from seasonal data. For identification of bird species found in each group see Table 5.

despite the low number of species present and the narrow resource spectrum.

Second, although the bird species pool rapidly increases in the early spring (up to 48),

not all the vegetation has emerged by May, nor are insects yet very abundant. Thus, the strain upon available food resources should encourage broad niche widths and considerable niche overlap at that time, which is what our data show. Moreover, as the summer fruits and leaves appear, resources increase; but so do the numbers of newly fledged young, and niche widths drop only slightly. By the time of our fall census in November, the species pool is drastically reduced, and seeds are abundant; thus species can be much more selective and narrow their niche width.

ACKNOWLEDGMENTS

We thank Hal L. Black, Thomas L. Thunrow, and John A. Fairchild for their help in

TABLE 5. Bird species grouped by cluster analysis of niche overlaps (Data from seasonal information). Table corresponds to Figure 8.

Group	Species	Group	Species
1	Audubon's Warbler Black-capped Chickadee Black-headed Grosbeak Western Bluebird Black-chinned Hummingbird Cassin's Kingbird Gray Flycatcher Lesser Goldfinch Red Crossbill Virginia's Warbler Western Tanager	3	Band-tailed Pigeon Brown-headed Cowbird Gray-headed Junco Common Grosbeak Mountain Bluebird Vesper Sparrow Yellow Warbler Yellow-rumped Warbler Orange-crowned Warbler Red-breasted Nuthatch Ruby-crowned Kinglet Swainson's Thrush Wilson's Warbler Yellow-bellied Sapsucker
2	Rufous-sided Towhee Say's Phoebe Common Bushtit Cooper's Hawk Violet-green Swallow Hermit Thrust Blue-gray Gnatcatcher Solitary Vireo Green-tailed Towhee White-throated Swift Bewick's Wren Western Flycatcher MacGillivray's Warbler Warbling Vireo Downy Woodpecker Traill's Flycatcher Black-throated Gray Warbler Mourning Dove House Wren Chipping Sparrow Ash-throated Flycatcher Broad-tailed Hummingbird Canyon Wren Rock Wren	4	Scrub Jay White-breasted Nuthatch Common Flicker Hairy Woodpecker Plain Titmouse Raven House Finch Robin Mountain Chickadee
		5	Black-billed Magpie Sharp-shinned Hawk Dark-eyed Junco Stellar's Jay
		6	Cassin's Finch Golden-crowned Kinglet Brown Creeper Pinyon Jay

data collection and Clayton M. White and Jerran T. Flinders for their constructive review of the manuscript.

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TABLE 6. Bird species grouped by cluster analysis of niche overlaps (data from season and habitat information). Table corresponds to Figure 9.

Group	Species	Group	Species
1	Black-headed Grosbeak Western Tanager Cooper's Hawk MacGillivray's Warbler Warbling Vireo Western Flycatcher Virginia's Warbler Traill's Flycatcher	6	Rufous-sided Towhee Broad-tailed Hummingbird Violet-green Swallow White-throated Swift Hairy Woodpecker Plain Titmouse House Finch Raven White-breasted Nuthatch Mountain Chickadee Dark-eyed Junco Pinyon Jay
2	Brown-headed Cowbird Yellow-rumped Warbler House Wren Rock Wren Ash-throated Flycatcher Black-throated Gray Warbler Blue-gray Gnatcatcher Canyon Wren	7	Chipping Sparrow Scrub Jay
3	Bewick's Wren Downy Woodpecker Common Bushtit Mourning Dove Black-billed Magpie Sharp-shinned Hawk Stellar's Jay Common Flicker Robin	8	Gray-headed Junco Red-breasted Nuthatch
4	Band-tailed Pigeon Common Grosbeak Orange-crowned Warbler Swainson's Thrush Yellow Warbler Yellow-bellied Sapsucker Wilson's Warbler	9	Ruby-crowned Kinglet Vesper Sparrow Mountain Bluebird
5	Black-chinned Hummingbird Green-tailed Towhee Solitary Vireo	10	Black-capped Chickadee Cassin's Kingbird Red Crossbill Lesser Goldfinch
		11	Brown Creeper
		12	Cassin's Finch Golden-crowned Kinglet
		13	Gray Flycatcher Western Bluebird Audubon's Warbler

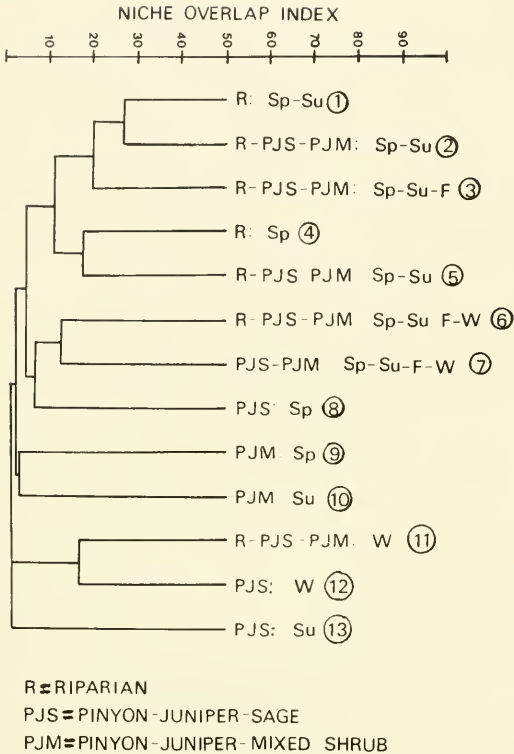


Fig. 9. Dendrogram of cluster analysis of 66 bird species by niche overlap habitat and seasonal data. For identification of bird species found in each group see Table 6.



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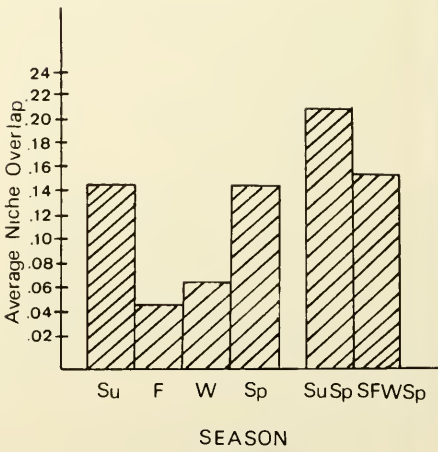


Fig. 10. Histograms comparing average niche breadths and average niche overlaps of bird species by season.

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APPENDIX

Navajo National Monument
Field Bird Checklist*

STATUS

- S = Spring
- Su = Summer
- F = Fall
- W = Winter
- H = General habitat preferences

HABITAT TYPE

- PJ = Pinyon-Juniper and sagebrush
- SI = Slickrock and canyon escarpment creek bottom
- R = Riparian (aspen-oaks along creek bottom)
- G = General distribution throughout the park

ABUNDANCE

- c = common; easily found in proper habitat in the right season.
- f = fairly; may be found in low numbers scattered through the proper habitat in the right season.

- u = uncommon; present but not easily found.
- o = occasional; unpredictable occurrence, seen only a few times during a season.
- r = rare; seen at intervals of two to five years.

SPECIES	STATUS AND ABUNDANCE				
	S	Su	F	W	H
Turkey Vulture	c	c			G
Cooper's Hawk	u	u	u		R
Sharp-shinned Hawk	u	u	u		R
Red-tailed Hawk	u	u	u	u	G
Swainson's Hawk	o	o	o		G
Golden Eagle	o	o	o	o	G
Prairie Falcon	r	r	o	r	G
Merlin	r		r		R
American Kestrel	f	f	u	o	G
Gambel's Quail	o	o	o	o	R
Killdeer	r	r	r		R
Solitary sandpiper	r		r		R
Spotted Sandpiper	r	r	r		R

*This checklist includes the 72 species listed on "Checklist of Birds, Navajo National Monument, Arizona" as well as 63 additional species observed in the present study.

SPECIES	STATUS AND ABUNDANCE					SPECIES	STATUS AND ABUNDANCE				
	S	Su	F	W	H		S	Su	F	W	H
Ring-billed Gull	r		r		G	Stellar's Jay	u	u	f	r	G
Band-tailed Pigeon	u	u			R	Scrub Jay	c	c	c	f	G
Rock Dove	o	o	o	r	S	Pinyon Jay	u	u	u	f	PJ
Mourning Dove	c	c	c	o	G	Black-billed Magpie	o	o	o	o	G
						Clark's Nutcracker	r	r	r	r	G
Yellow-billed Cuckoo		u			G	Common Raven	c	c	c	c	G
						Common Crow	u	o	u	o	G
Screech Owl	u	u	u	u	G	Black-capped Chickadee	o	o	o	o	G
Great Horned Owl	f	f	f	f	G	Mountain Chickadee	c	c	c	c	G
Long-eared Owl	o	o	o	o	G	Plain Titmouse	c	c	c	c	PJ
Spotted Owl	o	o	o	o	G	Common Bushtit	c	c	u	o	PJ
Saw-whet Owl	r		r	r	G	White-breasted Nuthatch	f	f	f	f	PJ
Flammulated Owl	u	u	u		G	Red-breasted Nuthatch	u	u	u	u	G
Pygmy Owl	o	o	o	o	G	Pygmy Nuthatch	o	o	o	o	PJ
Poor-will		f			G	Brown Creeper	o	r	u	f	G
Common Nighthawk		f			G						
Lesser Nighthawk		u			G	House Wren	f	f	u		R
White-throated Swift	f	f	u		G	Bewick's Wren	f	f	u	r	G
						Canyon Wren	f	f	u	u	SI
Broad-tailed Hummingbird	c	c	u		G	Rock Wren	f	f	u	u	SI
Calliope Hummingbird	o		o		G						
Black-chinned Hummingbird	u	f	u		G	Mockingbird		o			PJ
Rufous Hummingbird	r		r		G	Sage Thrasher	o		o		PJ
						Robin	f	f	f		R
Common Flicker	c	c	f	r	G	Townsend's Solitaire	o	o	o	o	G
Lewis' Woodpecker	r	o	r		R	Hermit Thrust	c	c	u		R
Yellow-bellied Sapsucker	u		u	r	R	Swainson's Thrush	u		u		R
Williamson's Sapsucker	o	o	o	r	G	Western Bluebird	u	u	o		PJ
Hairy Woodpecker	c	c	c	c	G	Mountain Bluebird	u	u	u	r	PJ
Downy Woodpecker	c	c	c	c	G						
Western Kingbird		f			G	Blue-gray Gnatcatcher	f	c	u		G
Cassin's Kingbird		f			G	Golden-crowned Kinglet	o		o	u	PJ
Ash-throated Flycatcher	c	c	f		G	Ruby-crowned Kinglet	f	o	f		G
Black Phoebe		o			R	Bohemian Waxwing				r	PJ
Say's Phoebe		o			R	Cedar Waxwing	o		o	o	PJ
Willow Flycatcher	f	f	u		G						
Hammond's Flycatcher	u	u	u		PJ	Northern Shrike				r	G
Dusky Flycatcher	u	f	u		PJ	Loggerhead Shrike	u	u	u	o	G
Western Flycatcher	u	f	u		R						
Olive-sided Flycatcher	u	u	u		R	Starling	o	o	o	o	Ca
Barn Swallow		o			SI						
Cliff Swallow		o			SI	Solitary Vireo	c	c	u		R
Violet-green Swallow	c	c	c		G	Warbling Vireo	u	f			R

SPECIES	STATUS AND ABUNDANCE					SPECIES	STATUS AND ABUNDANCE				
	S	Su	F	W	H		S	Su	F	W	H
Orange-crowned Warbler	u	r	u		R	Purple Finch			r		R
Virginia's Warbler	f	c	u		R	Cassin's Finch	u	o	u	f	G
Yellow Warbler	f	c	u		R	House Finch	f	f	f	f	G
Yellow-rumped Warbler	c	f	c		G	Pine Grosbeak				r	
Black-throated Gray Warbler	f	c	u		PJ	Pine Siskin	u		u	u	G
Yellowthroat	f	f	u		R	American Goldfinch	u	o	u	u	G
Yellow-breasted Chat	u	f	o		R	Lesser Goldfinch	u	f	u		SI
MacGillivray's Warbler	f	f	f		R	Red Crossbill	r	r	r	r	PJ
Wilson's Warbler	f		f		R	Green-tailed Towhee	f	f	f		R
						Rufous-sided Towhee	c	c	c	o	R
House Sparrow	u	u	u	u	G	Brown Towhee	o	o			G
Western Meadowlark	u	u	u	u	G	Savannah Sparrow	o	o	o		R
Red-winged Blackbird	u	u	u		G	Vesper Sparrow	o	o	o		G
Brewer's Blackbird	u	u	u		G	Lark Sparrow	u	u	u		PJ
Brownheaded Cowbird	f	f	u		G	Black-throated Sparrow	o	o	o		PJ
Bullock's Oriole	u	f	u		R	Sage Sparrow	o	o	o		PJ
Western Tanager	u	f	u		G	Dark-eyed Junco	f	f	c	c	G
Black-headed Grosbeak	u	f	u		R	Gray-headed Junco	u	u	u	u	PJ
Evening Grosbeak	o	o	o	u	G	Chipping Sparrow	c	c	c	o	PJ
Blue Grosbeak		r			R	Brewer's Sparrow	o	u	o		PJ
Lazuli Bunting	o	o	o		R	White-crowned Sparrow	f		f	u	G
						Fox Sparrow	u		u	o	G
						Lincoln's Sparrow	o	u	o		R
						Song Sparrow	o		o	o	R

REPRODUCTION IN *HYPSIGLENA*

Wilmer W. Tanner¹ and John R. Ottley²

ABSTRACT.— A clutch of 8 eggs was incubated. Three hatchlings emerged and were weighed, measured and color pattern indicated.

Although several reports have furnished information concerning the size, number, and weight of the eggs of the Night Snake, *Hypsiglena torquata* (Hibbard 1937, Tanner 1944-46, Wright and Wright 1957), there is little information on the time required for incubation and the size of new hatchlings.

A large specimen (568 mm) taken in the vicinity of Ortiz, Sonora, Mexico, by the junior author on 12 August 1979 laid eight eggs 28 August. A ninth egg was layed approximately one week later, but was eaten by a male *H. torquata* sharing the same cage. Although we have collectively examined or collected hundreds of individuals of this genus, this is our first opportunity to examine fresh eggs in the laboratory and to have a successful incubation. The eggs averaged approximately 26.5 mm long and weighed an average of about 1.77 grams. They varied in size, with one being only about half the size of the largest. Unfortunately, only the average size and weight was recorded.

Eggs were placed in a gallon jar on moist newspaper 28 August; two hatched 25 October and one 27 October. Incubation time was

59 days at room temperature, 68 to 75 F. Several eggs developed to near hatching and may have been unable to tolerate the low temperature of 68 degrees Fahrenheit. Data on the three hatchlings are presented in Table 1.

The scale patterns were within the ranges previously indicated for our series from Sonora (Tanner 1981). The nape pattern was typical for specimens seen from central Sonora, there being no indication of the light band. Two hatchlings had three nape spots with the median narrow and not extending completely between the large lateral spots. In the third, the spots were connected to form an irregular, incised band.

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TABLE 1. Basic data on the three eggs that hatched and size and pattern of the hatchlings.

BYU No.	Sex	Egg Length	Date Hatched	Length		Wt-gr	Dorsal spots
				S-V	Tail		
34772	♀	28.5 mm	25 Oct.	145	31	2.1	53
34773	♂	24.0 mm	25 Oct.	141	31	1.2	60
34774	♀	27.0 mm	27 Oct.	159	30	2.0	63

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**CHRYSOTHAMNUS NAUSEOSUS SSP. IRIDIS (ASTERACEAE):
A NEW ENDEMIC FROM UTAH**

Loran C. Anderson¹

ABSTRACT.— *Chrysothamnus nauseosus* ssp. *iridis* was named from material taken in Sevier County, Utah.

The Rainbow Hills, southeast of Sigurd in Sevier County, Utah, are of considerable interest biologically. Several plant species are endemic to the area or have ranges that extend only slightly beyond. The list includes *Astragalus loanus* Barneby, *Cymopterus coulteri* (M. E. Jones) Mathias, *C. rosei* M. E. Jones, *Mentzelia argillacea* Darlington, *Phacelia utahensis* Voss, and *Townsendia aprica* Welsh & Reveal. Now, an endemic subspecies of *Chrysothamnus nauseosus* (rabbit brush) may be added to the group.

MATERIALS AND METHODS

All known collections of the new taxon were used for comparative floral morphology (prepared from five heads per collection as in Anderson, 1964). Materials for chromosome counts and anatomical study were preserved and processed as in earlier studies (Anderson 1966, 1970).

TAXONOMY AND MORPHOLOGY

Chrysothamnus nauseosus (Pallas) Britt. ssp. *iridis* L. C. Anderson, ssp. nov.

Frutices humiles et diffundentes usque ad 2 dm alti, stirpibus glauco-albis, sine ramis infra inflorescentiam; folia glauco-viridia, linearia, 2–4 cm longa, 1 mm lata, multo longiora internodis; inflorescentia cyma paniculata et conglobata; capitula 12–16 mm longa, bracteis glabris; disci florum 5, flavi, corollis 7.8–9 mm longis, lineis stigmaticis longioribus quam styli appendicibus; achenia glabra.

TYPE: Utah, Sevier Co., seepage area of E-facing slope underlaid by Arapian Shale,

elev. 5900 ft, Rainbow Hills, 4.5 mi SE of Sigurd, 26 Sep 1979, S. L. Welsh 19258 (BRY-holotype!, FSU!, isotypes widely distributed as *C. parryi* var. *attenuatus*).

Low, spreading shrub 1–1.5 (2) dm tall, stems grayish white, tomentose, ascending, branched from the base; leaves grayish white or green, alternate, entire, linear (2)2.5–3(4) cm long, 1 mm wide, tomentulose, tips mucronate; inflorescence a tightly congested paniculate cyme; heads (12)13–15(16) mm long, 2.3–2.9 mm wide, phyllaries 20–26, stramineous, ovate to lanceolate, glabrous with hyaline margins somewhat ciliate distally, tips acute to acuminate; disk flowers 5, yellow, corollas (7.8)8.2–8.7(9) mm long, lobes 1.5–1.8 mm long, lanceolate, slightly spreading; style 17–18.5 mm long, stigmatic lines shorter than style appendages (29–35 percent of style branch length); achenes cylindric, 6–7(8.5) mm long, glabrous, pappus 5.5–7.2 mm long; $n = 9$. Locally established on steep slopes of Rainbow Hills, Peterson Creek drainage, Sevier County, Utah.

Additional specimens examined: Type locality, 31 Aug 1980, L. C. Anderson 5110 (BRY, FSU).

Relationships of this new subspecies are with some of the other glabrous-achened taxa of *C. nauseosus* (ssp. *leiospermus* and ssp. *psilocarpus*), although in growth form and general appearance it does look somewhat like *C. parryi* ssp. *attenuatus*. The Rainbow Hills rabbitbrush has glabrous involucre like ssp. *leiospermus*, but more leaves and whitish tomentose stems like ssp. *psilocarpus*. Perhaps the more abundant foliage of ssp. *iridis* relates to greater moisture availability on the seepage area (see Anderson 1973). It is fur-

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ther distinguished from *ssp. leiospermus* in having longer involucre that contain more phyllaries, longer corollas, and longer corolla lobes that spread. The corolla lobes are straight or incurved in *ssp. leiospermus*. It also differs from *ssp. psilocarpus* in having longer heads with more phyllaries, slightly shorter corollas, and shorter stigmatic lines.

The new rabbitbrush is diploid ($n = 9$, Anderson 5110), as are all subspecies of *C. nauseosus* (Anderson 1966, 1980). Good bivalent formation occurs in meiosis; no micronucleoli were observed in microsporocytes as were seen in some other subspecies (Anderson 1980). Pollen stainability in aniline blue in lactophenol averaged 94.6 percent.

Floral anatomy is very similar to that found in other glabrous-achened subspecies in terms of abundance of vasculature and secretory canals, but it differs in pattern. Flower vasculature consists of five to usually six bundles in the ovary wall. Four phloic traces are directed toward the base of the style at the top of the achene, but two end blindly there. Five bundles supply the corolla and androecium; the sixth bundle serves as one of the two style traces (termed pattern "d" in Anderson 1970). This pattern of vascular transition for stylar supply is more frequent in other species of the genus than in *C. nauseosus*; it was previously only known for *C. n. ssp. ceruminosus*, which is not closely related to *ssp. iridis*. Trichomes (glandular villi) on the corolla tube are either larger (136–175 μm) or more abundant than those of *ssp. leiospermus* and *ssp. psilocarpus*.

Abundance and distribution of floral vasculature and secretory canals in *C. nauseosus ssp. iridis* are much like those of *ssp. psilocarpus*; both subspecies have more ovarian bundles in their achenes than does *ssp. leiospermus*, but the latter has greater amounts of floral secretory canals. The index of specialization (on a scale of 10) as determined from vasculature and secretory canal abundance (Anderson and Fisher 1970) ranges from 2.3–6.7 for *C. nauseosus*. Subspecies *leiospermus* and *psilocarpus* have indexes from 6.1–6.2, and *ssp. iridis* has an index of 6.2–6.3. They are closely related in that respect but are easily distinguished in overall morphology.

This Rainbow Hills rabbitbrush is unique in its very narrow habitat tolerance. Most *Chrysothamnus* taxa are noted for their great ecological amplitude (expressed in a great range of edaphic conditions and/or latitude and altitude). For example, *C. viscidiflorus ssp. viscidiflorus* in northern Washoe County, Nevada, occurs in the following: Newlands fine loam, pH 6.2–6.4; Olson gravelly fine sandy loam, pH 6.6–7.0; Karlo very stony silty clay, pH 7.5–8.0; Disabel silty clay loam, pH 8.2–8.4 (Summerfield, pers. comm.). All plants have similar morphology when grown in the same soil in the greenhouse. Subspecies *viscidiflorus* occurs from 34° to over 48° in latitude and 800–13,000 ft in elevation.

In *Chrysothamnus nauseosus*, some of the great range of adaptability is demonstrated with the following: alkalinity and salinity in soils tested for *ssp. consimilis* ranged from pH 5.6 to pH 8.6 and from ECE (mmhos/cm) of 0.2 to 250; those for *ssp. hololeucus* had pH of 6.5–8.9 and ECE of 0.1–6.3. *Chrysothamnus nauseosus ssp. iridis* was found exclusively on the rather barren seepage area (dry at flowering time) of about 1,000 sq. ft; the soil is highly gypsiferous. The typical sagebrush-shadscale vegetation surrounding the seepage contained *C. nauseosus ssp. consimilis* and *C. viscidiflorus ssp. puberulus*; *C. nauseosus ssp. leiospermus* was found on rhyolite cliffs a few hundred feet up the hillside. The extremely limited range of *C. nauseosus ssp. iridis* and associated endemism make the Rainbow Hills an area very worthy of conservation and protection.

ACKNOWLEDGMENTS

Dr. Stanley Welsh graciously took me to the type locality; Dr. Walter Forehand assisted with the Latin diagnosis. Native Plants, Inc., supplied soil analysis data for selected subspecies of *C. nauseosus*. This study was supported by National Science Foundation Grant DEB 80-21776.

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REPRODUCTION IN THE SNAKE *LAMPROPELTIS PYROMELANA*

Wilmer W. Tanner¹ and Douglas C. Cox¹

ABSTRACT.— Reproduction in *L. pyromelana infralabialis* Tanner is reported. Eggs were measured and weighed and incubation time and hatching reported. Hatchlings were measured and weighed, and feeding was observed.

On 21 May 1980 three *Lampropeltis pyromelana infralabialis* Tanner were observed in a small meadow in Pine Grove Canyon in the Wah Wah Mountains in western Beaver County, Utah. Two, a male and a female, were returned to the laboratory at Brigham Young University by Drs. Douglas C. Cox and Richard W. Baumann. On 24 June 1980, this female layed five eggs, each of which measured 4.7 to 4.11 mm in length and 1.9 to 1.72 mm in width, an average of 4.38 in length and 1.786 mm in width, total weight 46.67 grams or an average of 9.326 grams per egg. They were clustered and all adhering so that separation was not possible.

The eggs were placed in a container of damp vermiculite and potting soil mixed in styrofoam and kept at a temperature of 78 to 84 F. After a few days, they were transferred to the Venom Research Laboratory, Veterans Administration Medical Center, in Salt Lake City, where they were all successfully incubated by Mr. James L. Glenn, curator of the serpentarium.

Incubation required 57 to 58 days, with all hatchlings developing normally and without any physical impairments. The first hatchlings emerged on 19 August 1980, and the last on 20 August 1980. Table 1 provides the basic statistics.

The female parent, and additional specimens from the same area, had the scale patterns, measurements, and color patterns presented in Table 2 and Figure 1 and 2.

We returned the hatchlings to our (BYU) laboratory 1 September for feeding experiments. While at the serpentarium, two fed on newborn white mice. We found that they preferred small lizards such as hatchling *Uta* and *Sceloporus*. When these became scarce, an assistant curator (Mark Seward) discovered that pinkies (baby mice) would be readily taken if they were smeared with the juices of crushed lizards. By these methods all were feeding within a few days.

We are most grateful to James L. Glenn and his assistants for their aid, and to our museum staff (Mark Seward and Dr. Richard Baumann) for their interest and care in this project.

This record establishes a mountain chain type distribution from the mountains east of Beaver, to the Mineral range west of Beaver, to the Wah Wah range, and west to the Egan range east of Lund, Nevada. This is another example of a disjunct distribution that occurs in a number of the desert ranges of western Utah and most of Nevada. Such distributions undoubtedly developed when widespread species were forced from the valleys as this

TABLE 1. Measurements, weights and color pattern of five hatchling *Lampropeltis pyromelana infralabialis* Tanner.

No.	sex	Length in mm		weight in grams	Triads		white rings
		total	tail		body	tail	
1	♀	282	47	7.9	43	9	52
2	♂	277	47	7.4	36	10	45
3	♂	284	52	8.3	38	9	
4	♀	279	48	8.6	36	9	46
5	♂	294	60	9.0	42	10	52

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inland desert dried, and the only suitable where cooler and more moist habitats were habitat was in the higher mountain areas still available.

TABLE 2. Scale patterns, measurements, and color patterns for three adults.

Sex	Scale rows	Ventrals	Caudals	Labials		Length		White rings
				Upper	Lower	Body	Tail	
♀	23-23-19	224	64	7-7	9-9	705	136	43
♂	23-23-19	234	72	7-7	9-9	994	164	50
♂	23-23-17	230	74	7-7	9-9	736	154	48

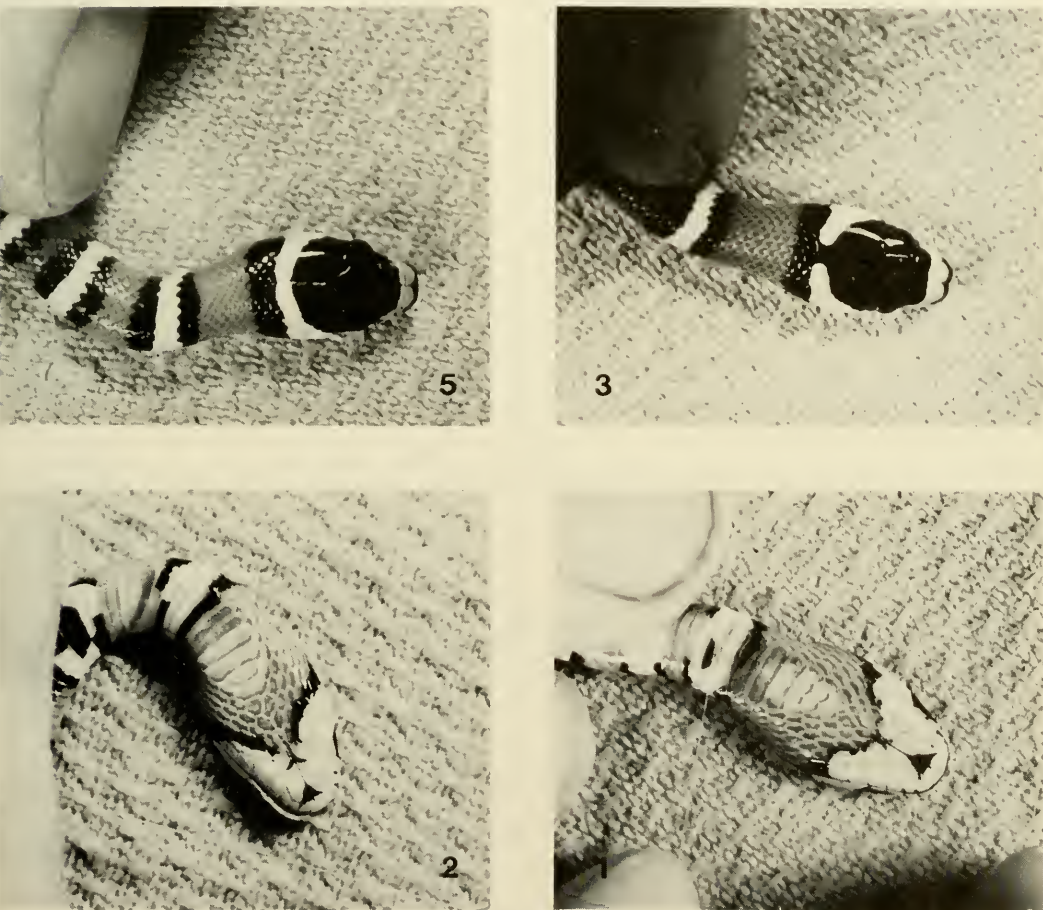


Fig. 1. Color pattern of head; specimens 1 and 2 ventral views; specimens 3 and 5 dorsal views.

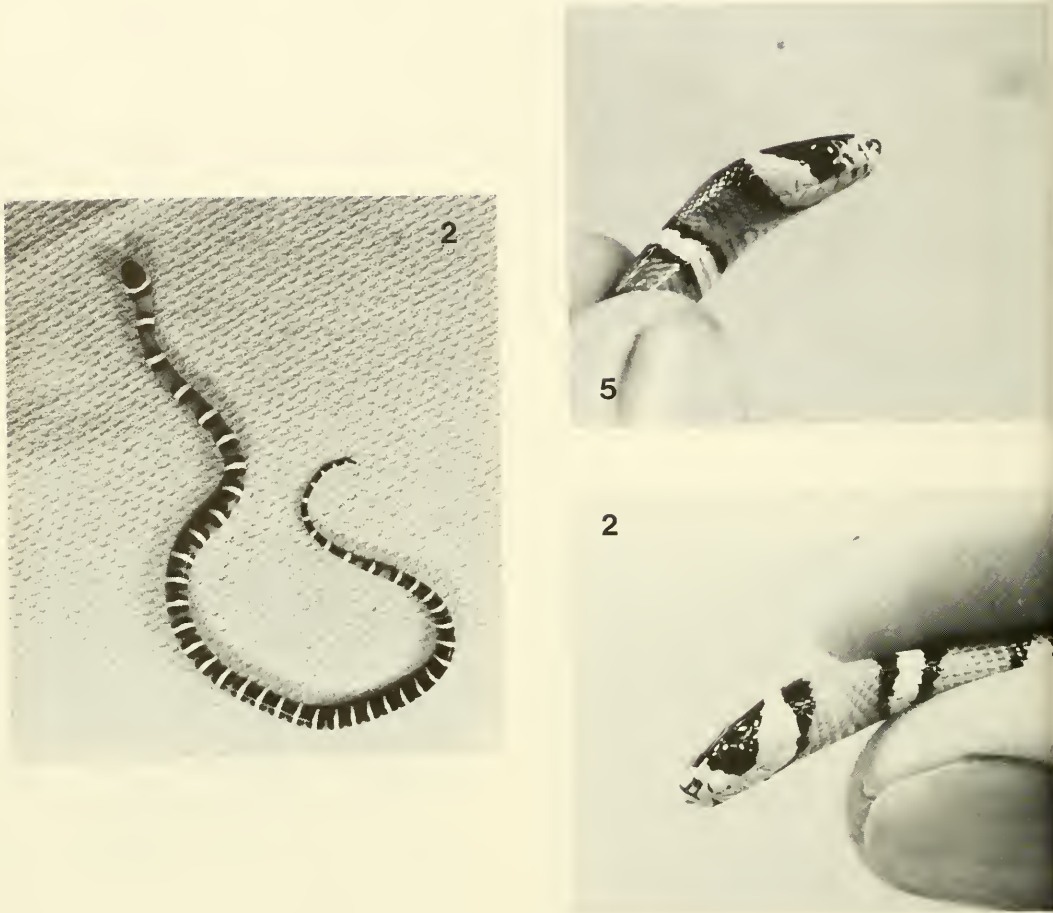


Fig. 2. Specimen 2 total body pattern; specimens 5 and 2 lateral view of head.

DIATOMS OF OREGON CAVES NATIONAL MONUMENT, OREGON

Larry L. St. Clair¹, Samuel R. Rushforth¹, and James V. Allen¹

ABSTRACT.— The diatom flora of the Oregon Caves National Monument, Josephine Co., Oregon, was investigated. Diatoms were distributed throughout the cave system with abundance and species diversity depending upon moisture, light, availability of mineral nutrients, and proximity to cave openings. Twenty-six taxa were identified and described.

Oregon Caves National Monument is 32 km southeast of Cave Junction on Oregon State Highway 46, Josephine County, Oregon (Map 1). The combined length of passages and rooms in the caves is approximately 1 km. The entrance of the caves is at an elevation of 1200 m within a natural tran-

sition zone between a lower elevation flora of mixed deciduous trees and shrubs and a higher elevation flora dominated by conifers.

The Oregon Caves are stratigraphically in a marble bed in the Applegate group. Applegate rocks are triassic in age and consist of interbedded sedimentary rocks and



Map 1. Oregon Caves National Monument is located in the Siskiyou National Forest, 32 kilometers southeast of Cave Junction, Oregon.

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volcanic ash and fragments (State of Oregon 1942). Shales, sandstones, and limestones of the Applegate group were metamorphosed and then uplifted to form part of the Klamath peneplane. Erosion of this peneplane formed the Klamath mountain system, which includes the Siskiyou Range and Oregon Caves. Cave formation in this system is similar to that of other localities, with extensive ground water erosion and associated deposition of calcium carbonate.

The caves were discovered by Elijah Davison in the fall of 1874. Nevertheless, it was not until 1909 that a tract of 195 hectares was set aside as Oregon Caves National Monument. Lighting in the caves was installed in 1932, which also marked the beginning of regular public visits.

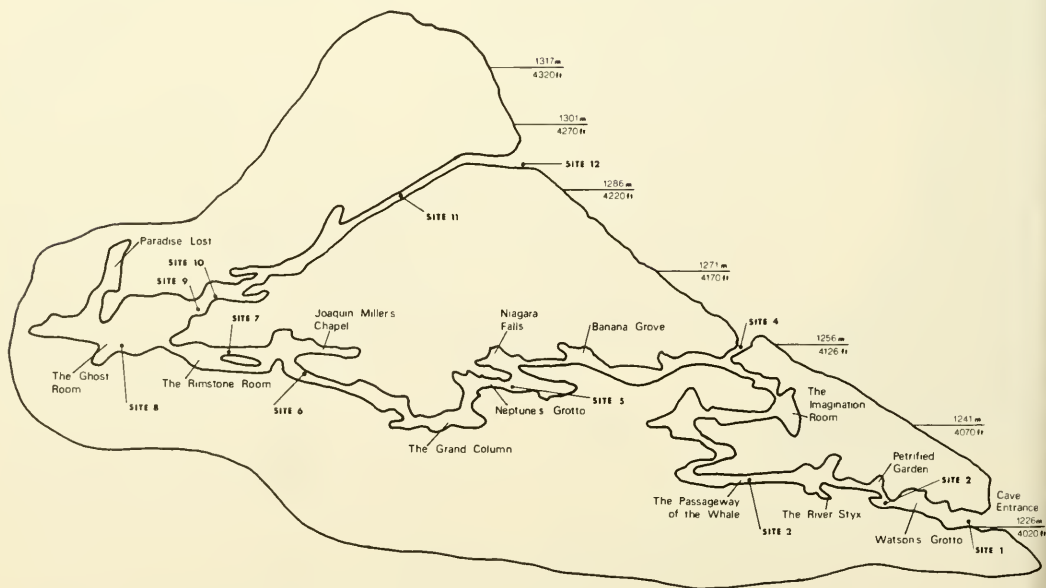
Shortly after the lighting system was installed, the development of moss gametophytes and algal incrustations on and near formations adjacent to light fixtures was observed. The encroachment of these organisms onto formations in the caves has resulted in the permanent discoloration of some formations, with probable physical degradation in some cases. The present study was initiated to determine the species of algae resident in the caves in order to provide baseline data for establishing management techniques for

controlling algal and moss growth on cave formations. This paper deals with the diatom species in the Oregon Caves system, with observations and comments on diatom distribution patterns.

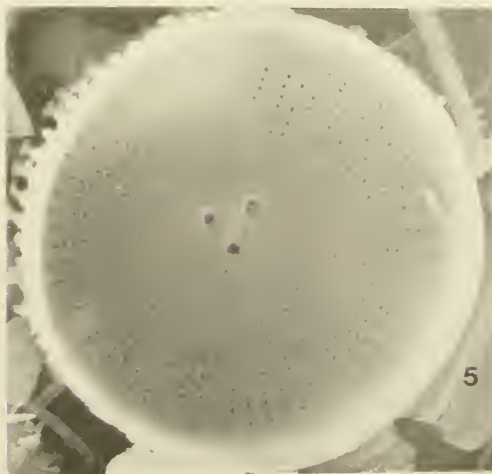
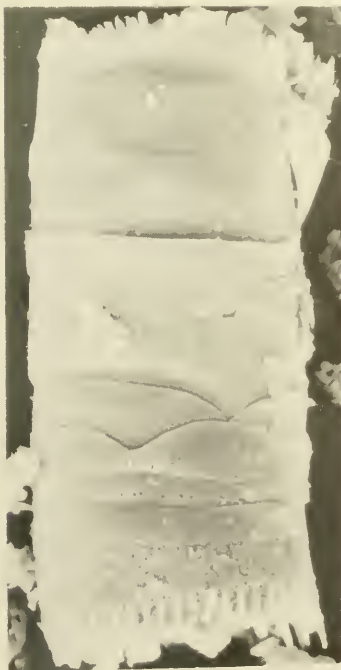
MATERIALS AND METHODS

One composite sample was collected from each of 12 sites located at regular intervals throughout the rooms and passageways of the cave on 28 April 1978. Samples were collected under sterile conditions, with presterilized instruments and collecting vials. Most samples consisted of scrapings from algal-moss associations adjacent to light fixtures. However, some scrapings were made of dry incrustated algae on cave formations and of mucilaginous material from several seep walls.

The 12 collecting sites (Map 2) were designated as follows: No. 1, scrapings from wall of cave entrance; No. 2, scrapings from wall and floor near light between Watson's Grotto and Petrified Gardens; No. 3, scrapings from wall in passageway of the Whale; No. 4, scrapings from wall and floor of the 110 exit; No. 5, scrapings from wall near light in passageway between Throne Room and Neptune's Grotto; No. 6, scrapings from Touching Post; No. 7, scrapings from wall



Map. 2. Twelve collection sites (represented by black dots) were established at regular intervals throughout the 1 km length of the cavern system.



Figs. 1-5. *Melosira roeseana*: 1, girdle view, light micrograph; 2, valve view, light micrograph; 3, girdle view, scanning electron micrograph (SEM); 4, oblique girdle view, SEM; 5, inner view of valve, SEM. All scales equal to 10 μ m.

and floor in Rhinestone Room; No. 8, scrapings from wall near light in Ghost Room; No. 9, scraping of slime accumulated on stair rail between Ghost Room and Wedding Cake Room; No. 10, scrapings from wall in Wedding Cake Room; No. 11, scrapings from wall and floor of exit tunnel; No. 12, scrapings from face of exit.

Wet mounts of each sample were prepared in order to determine whether or not viable diatoms were present. Living specimens were observed from all samples except sample No. 9. In several samples large numbers of living individuals were observed.

Standard methods for preparing diatom slides were used (St. Clair and Rushforth 1976). Portions of each sample were boiled in concentrated nitric acid and washed with distilled water. A small portion of the solution containing cleaned diatom frustules was dried on cover slips that were then mounted in Naphrax diatom mountant.

Identifications were made using a Zeiss RA microscope equipped with Normarski interference phase-contrast accessories. Photomicrographs were taken of each species using Nikon AFM photomicrographic accessories.

A second subsample of cleaned frustules was mounted on scanning electron microscope stubs. These were studied in an Amray 1000 scanning electron microscope. Photomicrographs were taken of each species observed.

RESULTS

Ten genera including 26 taxa were identified during this study (Table 1). These diatoms, described and discussed below, were identified from various locations throughout the rooms and connecting passageways of the Oregon Caves. A reference to a complete description is given for each species.

Melosira

Melosira roeseana Rabenhorst (Figs. 1-5). Diameter 19-33 μm ; striae 7-10 in 10 μm ; punctae distinct, 3-4 prominent punctae in center of valve (Hustedt 1930:93). It was common at the passageway between Watson's Grotto and the Petrified Gardens (Site 2), 110 exit (Site 4), exit tunnel (Site 11), and the face of the exit (Site 12).

TABLE 1. Phylogenetic list of diatoms (Division Basiliariophyta, Class Bassiliariophyceae) collected from the Oregon Caves National Monument.

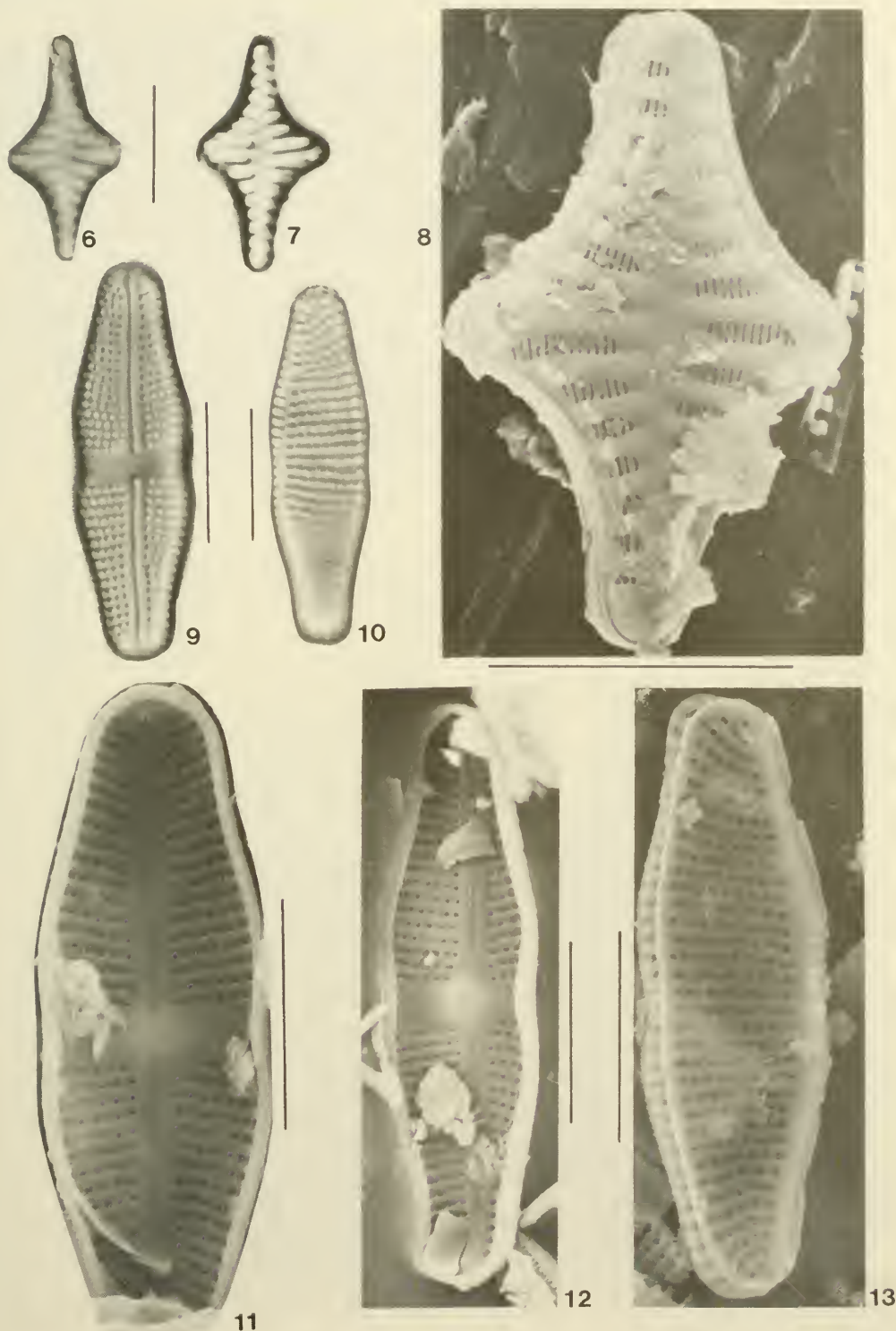
Order Rhizosoleniales
Family Coscinodiscaceae
<i>Melosira roeseana</i> Rabenhorst
Order Fragilariales
Family Fragilariaceae
<i>Fragilaria construens</i> (Ehr.) Grunow
Order Achnanthales
Family Achnanthaceae
<i>Achnanthes coarctata</i> (Breb. in W. Sm.) Grunow
<i>Achnanthes exigua</i> Grunow
<i>Achnanthes exigua</i> var. <i>heterovalva</i> Krasske
<i>Achnanthes lanceolata</i> (Breb.) Grunow
<i>Achnanthes microcephala</i> (Kutz.) Grunow
<i>Achnanthes minutissima</i> Kutzig
<i>Achnanthes montana</i> Krasske
Order Naviculales
Family Naviculaceae
<i>Diploneis oblongella</i> (Naeg. ex Kutz.) Ross
<i>Navicula brekkaensis</i> Petersen
<i>Navicula contenta</i> f. <i>biceps</i> Arnott
<i>Navicula cryptocephala</i> var. <i>veneta</i> (Kutz.) Rabenhorst
<i>Navicula gallica</i> var. <i>montana</i> Bahls
<i>Navicula insociabilis</i> Krasske
<i>Navicula minima</i> Grunow
<i>Navicula pelliculosa</i> (Breb. ex Kutz.) Hilse
<i>Navicula perpusilla</i> (Kutz.) Grunow
<i>Navicula pupula</i> var. <i>rectangularis</i> (Greg.) Grunow
<i>Navicula secura</i> Patrick
<i>Pinnularia</i> sp.
Family Cymbellaceae
<i>Cymbella minuta</i> var. <i>silesiaca</i> (Bleisch ex. Rabh.) Reimer
<i>Amphora perpusilla</i> (Grun.) Grunow
Order Bacillariales
Family Nitzschiaceae
<i>Hantzschia amphioxys</i> (Ehr.) Grunow
<i>Nitzschia linearis</i> (Agardh) Wm. Smith
<i>Nitzschia paleacea</i> Grunow

Fragilaria

Fragilaria construens (Ehr.) Grunow (Figs. 6-8). Length 19-20 μm ; width 9-12 μm ; striae 10-12 in 10 μm (Patrick and Reimer 1966:125). It was found at: tunnel between Watson's Grotto and the Petrified Gardens (Site 2), passageway between Throne Room and Neptune's Grotto (Site 5), and the Wedding Cake Room (Site 10).

Achnanthes

Achnanthes coarctata (Breb. in W. Sm.) Grunow (Figs. 9-13). Length 32-34 μm ; width 9-10 μm ; rapheless valve striae 12-14 in 10 μm ; raphe valve striae 12-16 in 10 μm



Figs. 6-13. Diatom spp.: 6-7, *Fragilaria construens* valve views, light micrographs; 8, *Fragilaria construens* valve view, SEM; 9, *Achnanthes coarctata* raphe valve view, light micrograph; 10, *Achnanthes coarctata* nonraphe valve, light micrograph; 11-12, *Achnanthes coarctata* raphe valve views, SEM; 13, *Achnanthes coarctata* nonraphe valve view, SEM. All scales equal to 10 μm.

(Patrick and Reimer 1966:277). It was found only at the exit tunnel (Site 11).

Achnanthes exigua Grunow (Figs. 14–17; 21). Length 12–15 μm ; width 5–6 μm ; rapheless valve striae 20–24 in 10 μm ; raphe valve striae 24–28 in 10 μm (Patrick and Reimer 1966:257). One of most common species in this study, it was identified from the following sites: tunnel between Watson's Grotto and Petrified Gardens (Site 2), Passageway of the Whale (Site 3), 110 exit (Site 4), passageway between the Throne Room and Neptune's Grotto (Site 5), the Rhinestone Room (Site 7), the Ghost Room (Site 8), the Wedding Cake Room (Site 10), the exit tunnel (Site 11), and the face of the exit (Site 12).

Achnanthes exigua var. *heterovalva* Krasske (Figs. 18–20). Length 7–10 μm ; width 4–5 μm ; raphe and rapheless valve striae 25–27 in 10 μm (Patrick and Reimer 1966:258). It was identified from the following sites: Passageway of the Whale (Site 3), passageway between the Throne Room and Neptune's Grotto (Site 5), the Rhinestone Room (Site 7), the Wedding Cake Room (Site 10), and the exit tunnel (Site 11).

Achnanthes lanceolata (Breb.) Grunow (Figs. 22–29). Length 9–15 μm ; width 4–5 μm ; rapheless valve striae 14–16 in 10 μm ; raphe valve striae 12–14 in 10 μm (Patrick and Reimer 1966:269). It was collected from the following sites: tunnel between Watson's Grotto and the Petrified Gardens (Site 2), Passageway of the Whale (Site 3), 110 Exit (Site 4), passageway between the Throne Room and Neptune's Grotto (Site 5), the Wedding Cake Room (Site 10), and the exit tunnel (Site 11).

Achnanthes microcephala (Kutz.) Grunow (Fig. 30). Length 7–8 μm ; width 2–3 μm ; striae about 30 in 10 μm on both valves, often not resolved (Patrick and Reimer 1966:250). Collected from the Passageway of the Whale (Site 3).

Achnanthes minutissima Kutzing (Figs. 31–32). Length 9–12 μm ; width 2–3 μm ; striae 30–32 in 10 μm on both valves (Patrick and Reimer, 1966:253). Common at all sites in the cave system except for Site 9, and the face of the exit (Site 12).

Achnanthes montana Krasske (Figs. 33–34, 40–41). Length 10–12 μm ; width 5–6

μm ; striae 18–20 in 10 μm on both valves (Hustedt 1930:204). It was identified from the following samples: passageway between Watson's Grotto and the Petrified Gardens (Site 2), Passageway of the Whale (Site 3), 110 exit (Site 4), passageway between the Throne Room and Neptune's Grotto (Site 5), and the Rhinestone Room (Site 7).

Diploneis

Diploneis oblongella (Naeg. ex Kutz.) Ross (Figs. 36–39). Length 10–26 μm ; width 7–8 μm ; costae 14–20 in 10 μm (Patrick and Reimer 1960:413). Identified from two sites, the Wedding Cake Room (Site 10) and the exit tunnel (Site 11).

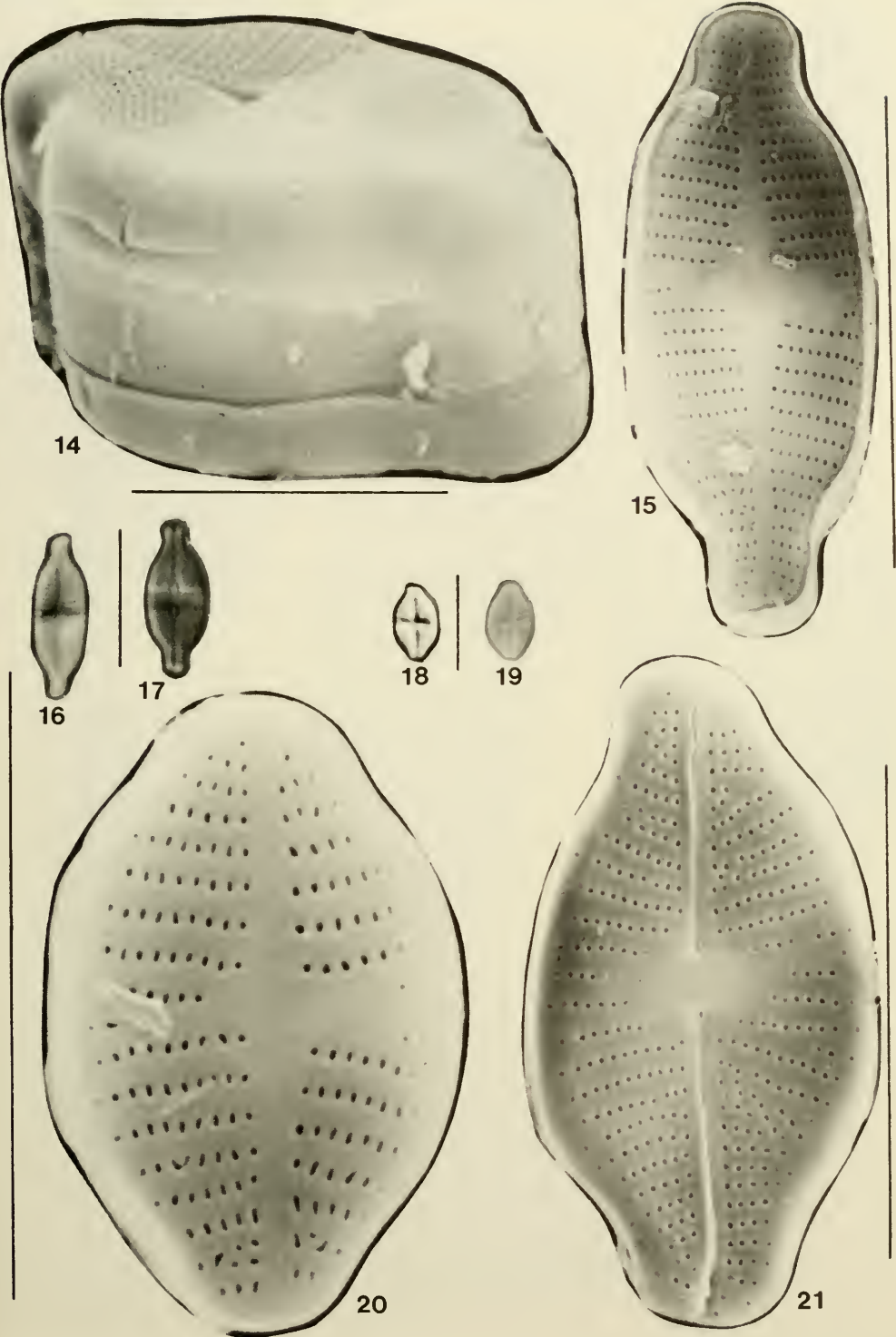
Navicula

Navicula brekkaensis J. B. Petersen (Figs. 55–57). Length 9–15 μm ; width 2–3 μm ; striae about 35 in 10 μm (Hustedt 1960–1966:221). Taken in the passageway between the Throne Room and Neptune's Grotto (Site 5).

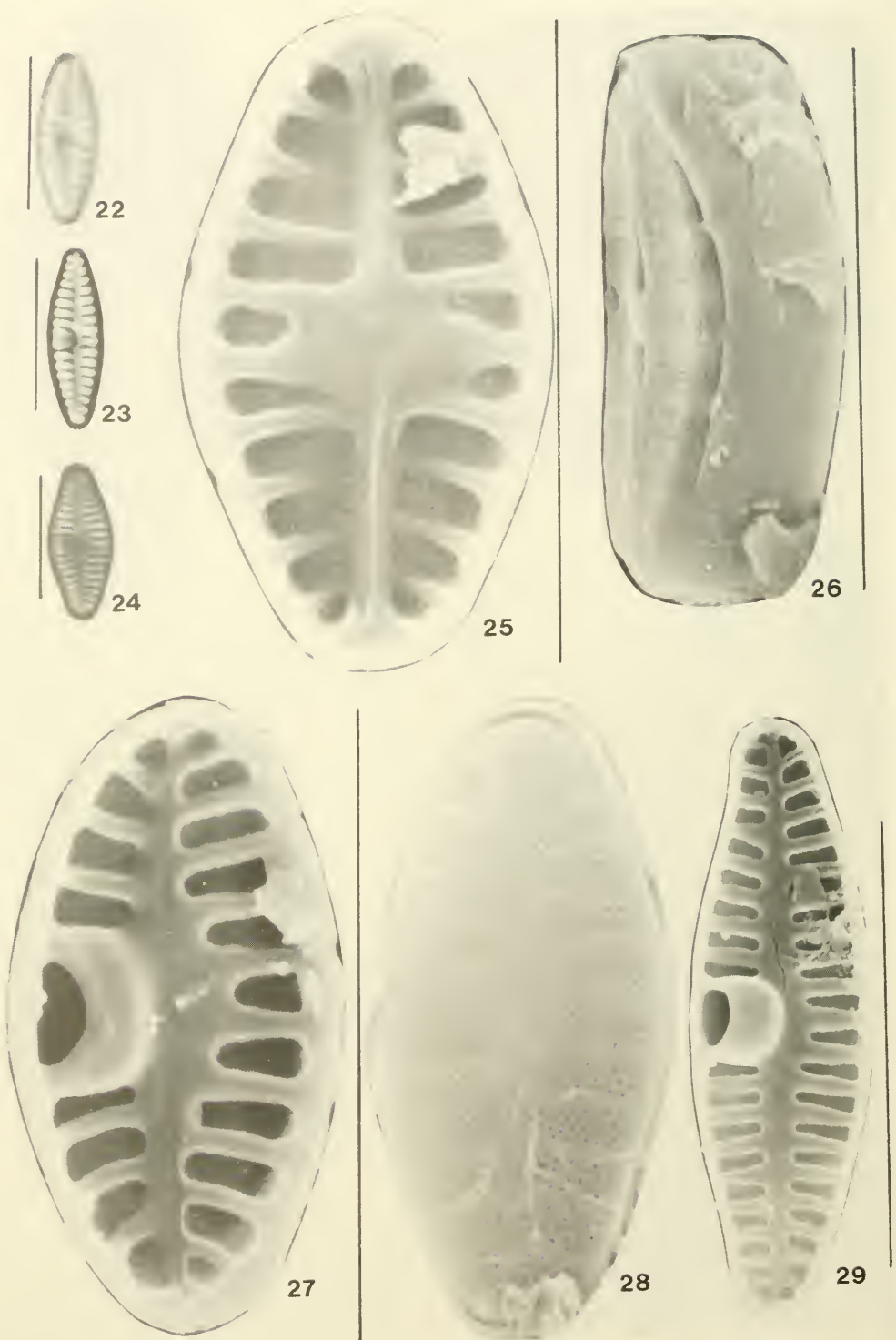
Navicula contenta f. *biceps* Arnott (Figs. 62–68). Length 10–16 μm ; width 3–4 μm ; striae 33–36 in 10 μm (Hustedt 1930:277). Common throughout the cave system and at all sites except for the passageway between the Throne Room and Neptune's Grotto (Site 5), the Rhinestone Room (Site 7), Site 9 and the Wedding Cake Room (Site 10).

Navicula cryptocephala var. *veneta* (Kutz.) Rabenhorst (Figs. 59–61). Length 20–25 μm ; width 5–6 μm ; striae 15–18 in 10 μm (Patrick and Reimer 1966:504). Rare from samples collected in the Wedding Cake Room (Site 10).

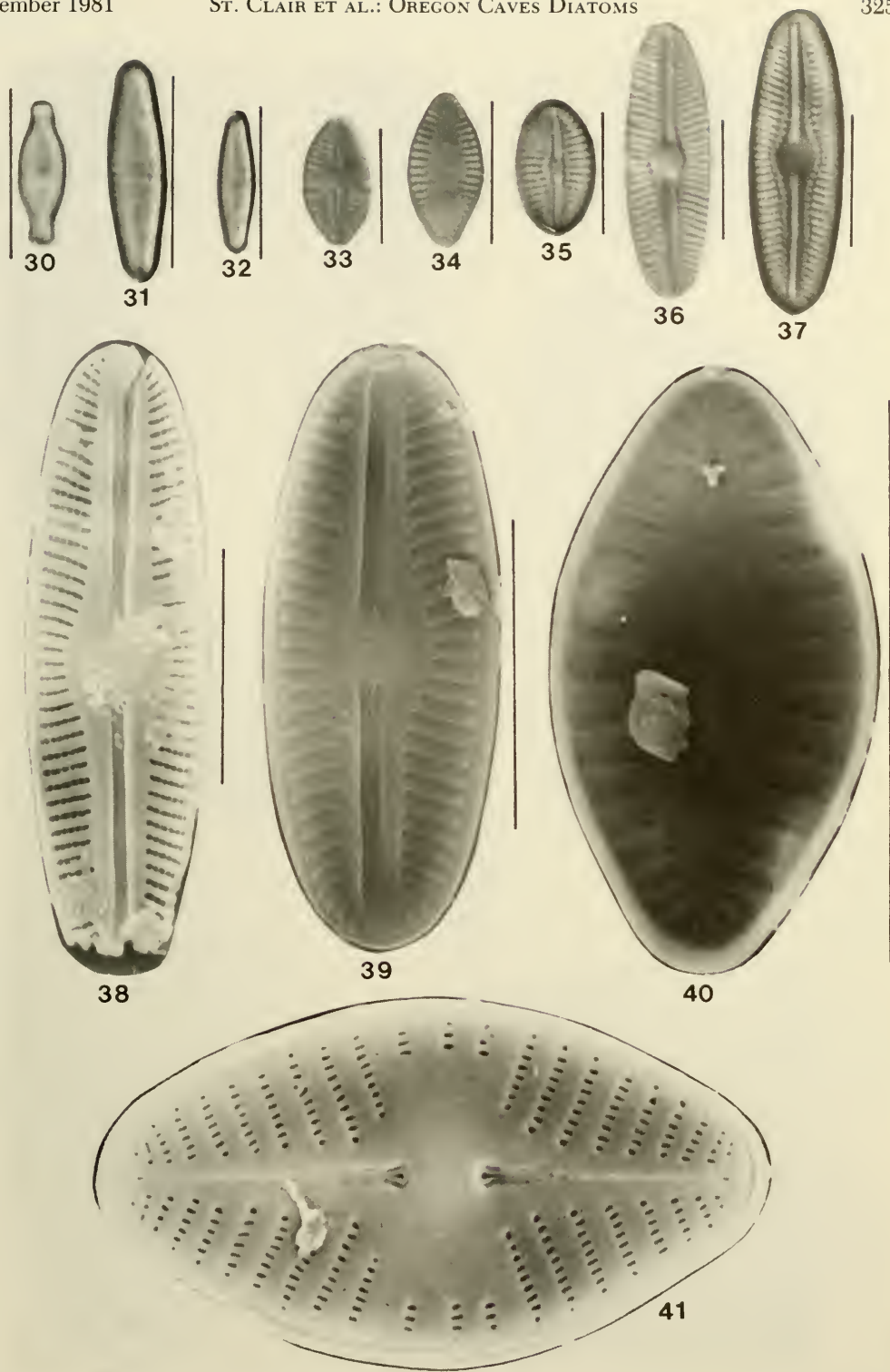
Navicula gallica var. *montana* Bahls (Figs. 42–48, 53). Length 12–19 μm ; width 3–4 μm ; striae 28–38 in 10 μm (Bahls 1981:14). At all sites except Site 9. This taxon was recently named from specimens collected from Lewis and Clark Caverns, Montana, by Loren Bahls (1981). We have used the name based on the lanceolate axial area and the length. Some of our specimens, however, have finer striae than either the nominate or variety of this taxon, ranging into the striae range of *N. fragilarioides*. Even so, the striae range appeared to be continuous and we chose to place our specimens in a single taxon.



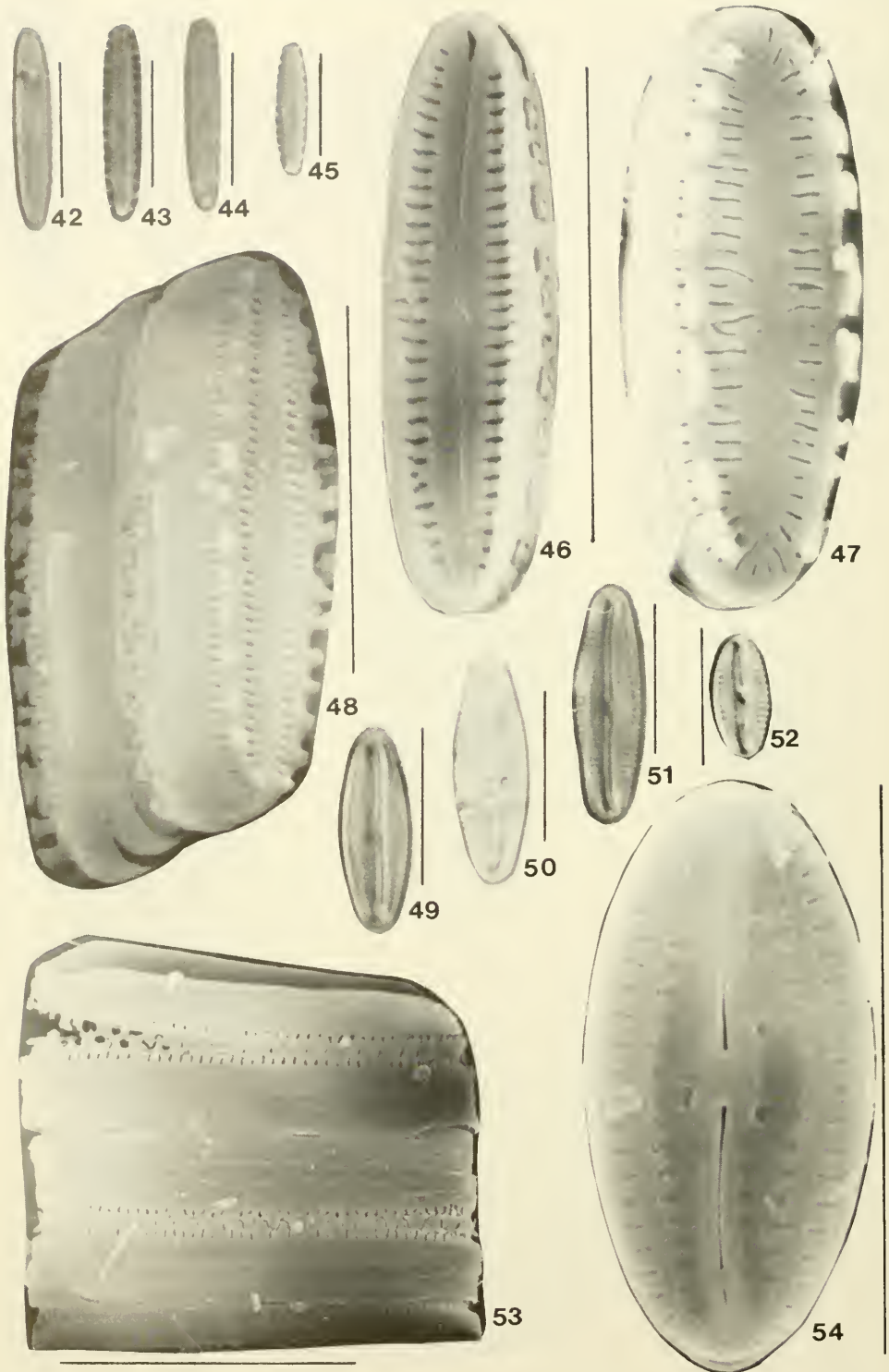
Figs. 14-21. *Achnanthes* spp.: 14, *Achnanthes exigua* oblique view of raphe valve, SEM; 15, *Achnanthes exigua* nonraphe valve, SEM; 16, *Achnanthes exigua* nonraphe valve, light micrograph; 17, *Achnanthes exigua* raphe valve, light micrograph; 18-19, *Achnanthes exigua* var. *heterovalva* nonraphe valve views, light micrographs; 20, *Achnanthes exigua* var. *heterovalva* nonraphe valve, SEM; 21, *Achnanthes exigua* raphe valve, SEM. All scales equal to 10 μ m.



Figs. 22-29. *Achnanthes lanceolata*: 22, raphe valve, light micrograph; 23-24, nonraphe valves, light micrographs; 25, inner view of raphe valve, SEM; 26, oblique view of frustule, SEM; 27, inner view of nonraphe valve, SEM; 28, outer view of nonraphe valve, SEM; 29, inner view of nonraphe valve, SEM. All scales equal to 10 μ m.



Figs. 30-41. *Achnanthes* spp. and *Diploneis* sp.: 30, *A. microcephala* raphe valve, light micrograph; 31-32, *A. minutissima* raphe valves, light micrographs; 33, *A. montana* raphe valve, light micrograph; 34, *A. montana* nonraphe valve, light micrograph; 35-37, *D. oblongella* valve views, light micrographs; 38-39, *D. oblongella* valve views, SEM; 40, *A. montana* nonraphe valve, SEM; 41, *A. montana* raphe valve, SEM. All scales equal to 10 μ m.



Figs. 42-54. *Navicula* spp.: 42-45, *N. gallica* var. *montana* valve views, light micrographs; 46-47, *N. gallica* var. *montana* valve views, SEM; 48, *N. gallica* var. *montana* oblique view showing two frustules, SEM; 49-52, *N. insociabilis* valve views, light micrographs; 53, *N. gallica* var. *montana* girdle view showing several joined frustules, SEM; 54, *N. insociabilis* valve view, SEM. All scales equal to 10 μ m.

Navicula insociabilis Krasske (Figs. 49–52, 54). Length 9–16 μm ; width 5–6 μm ; striae 23–26 in 10 μm (Hustedt 1960–1966:181). Collected from the tunnel between Watson's Grotto and the Petrified Gardens (Site 2), the 110 Exit (Site 4), the Wedding Cake Room (Site 10), and the exit tunnel (Site 11).

Navicula minima Grunow (Figs. 71–72). Length 9–11 μm ; width 4–5 μm ; striae 24–30 in 10 μm (Patrick and Reimer 1966:488). Collected from the tunnel between Watson's Grotto and the Petrified Gardens (Site 2) and the 110 Exit Site (Site 4).

Navicula pelliculosa (Breb. ex Kutz.) Hilse (Figs. 73–74, 80). Length 5–11 μm ; width 3 μm ; striae unresolved (Patrick and Reimer 1966:484). Identified from the Passageway of the Whale (Site 3) and the Touching Post (Site 6).

Navicula perpusilla (Kutz.) Grunow (Fig. 69–70, 75–76). Length 9–11 μm ; width 3–5 μm ; striae 31–33 in 10 μm (Patrick and Reimer 1966:478). Identified from the entrance (Site 1), the tunnel between Watson's Grotto and the Petrified Gardens (Site 2), the 110 Exit (Site 4), and the Touching Post (Site 6).

Navicula pupula var. *rectangularis* (Greg.) Grunow (Fig. 58). Length 25 μm ; width 7 μm ; striae 14–15 in 10 μm (Patrick and Reimer 1966:497). Collected only from the face of the exit (Site 12).

Navicula secura Patrick (Figs. 77–79, 81–82). Length 10–14 μm ; width 3–4 μm ; striae 30–38 in 10 μm (Patrick and Reimer 1966:490). Collected from the entrance (Site 1), the tunnel between Watson's Grotto and the Petrified Gardens (Site 2), the Passageway of the Whale (Site 3), the 110 Exit (Site 4), and the passageway between the Throne Room and Neptune's Grotto (Site 5). Several of our specimens have somewhat coarser striae than those described by Patrick (1959).

Pinnularia

Pinnularia sp. 1 (Figs. 83–87). Valve 23–30 μm long by 4–5 μm wide, linear to slightly linear-elliptical; apices rounded to slightly rostrate; raphe linear, simple, proximal ends curved in same direction; axial area narrow, becoming broader near the central area; central area a broad transverse fascia; striae radiate, becoming convergent toward apices, 16–28 in 10 μm . Collected from

the passageway between the Throne Room and Neptune's Grotto (Site 5), the Wedding Cake Room (Site 10), and the exit tunnel (Site 11). This species was also collected in the Timpanogos Cave System, Utah Co., Utah, and at that time was identified as *Pinnularia intermedia* (Lagerst) Cleve. The striae count, however, is significantly finer in our specimens than in descriptions for *P. intermedia*.

Cymbella

Cymbella minuta var. *silesiaca* (Bleisch ex. Rabh.) Reimer (Figs. 88–89). Length 20–22 μm ; width 5–6 μm ; dorsal striae 14 in 10 μm ; ventral striae 14–18 in 10 μm (Patrick and Reimer 1975:49). Identified from the tunnel between Watson's Grotto and the Petrified Gardens (Site 2) and the Wedding Cake Room (Site 10).

Amphora

Amphora perpusilla (Grun.) Grunow (Fig. 90). Length 9–12 μm ; width 3 μm ; striae 16–17 in 10 μm (Patrick and Reimer 1975:70). Collected only from the passageway between the Throne Room and Neptune's Grotto (Site 5).

Hantzschia

Hantzschia amphioxys (Ehr.) Grunow (Figs. 94–95). Length 55–64 μm ; width 6–7 μm ; fibulae 7–9 in 10 μm ; striae 24–28 in 10 μm (Hustedt 1930:393). Collected from the exit tunnel (Site 11) and the face of the exit (Site 12).

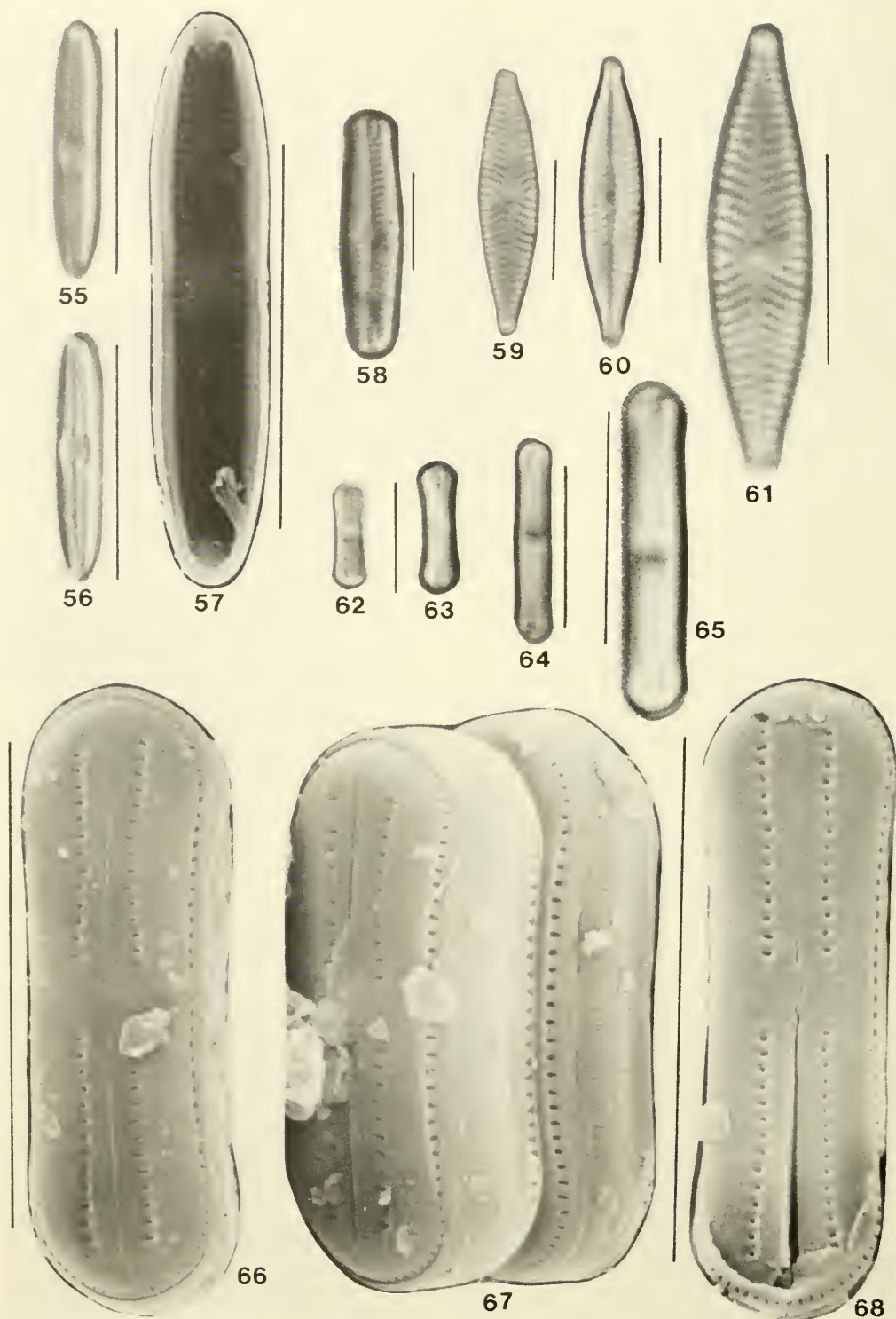
Nitzschia

Nitzschia linearis (Agardh) Wm. Smith (Figs. 91–93). Length 75–78 μm ; width 5–6 μm ; fibulae 8–12 in 10 μm ; striae 28–32 in 10 μm (Hustedt 1930:409). Collected from the exit tunnel (Site 11) only.

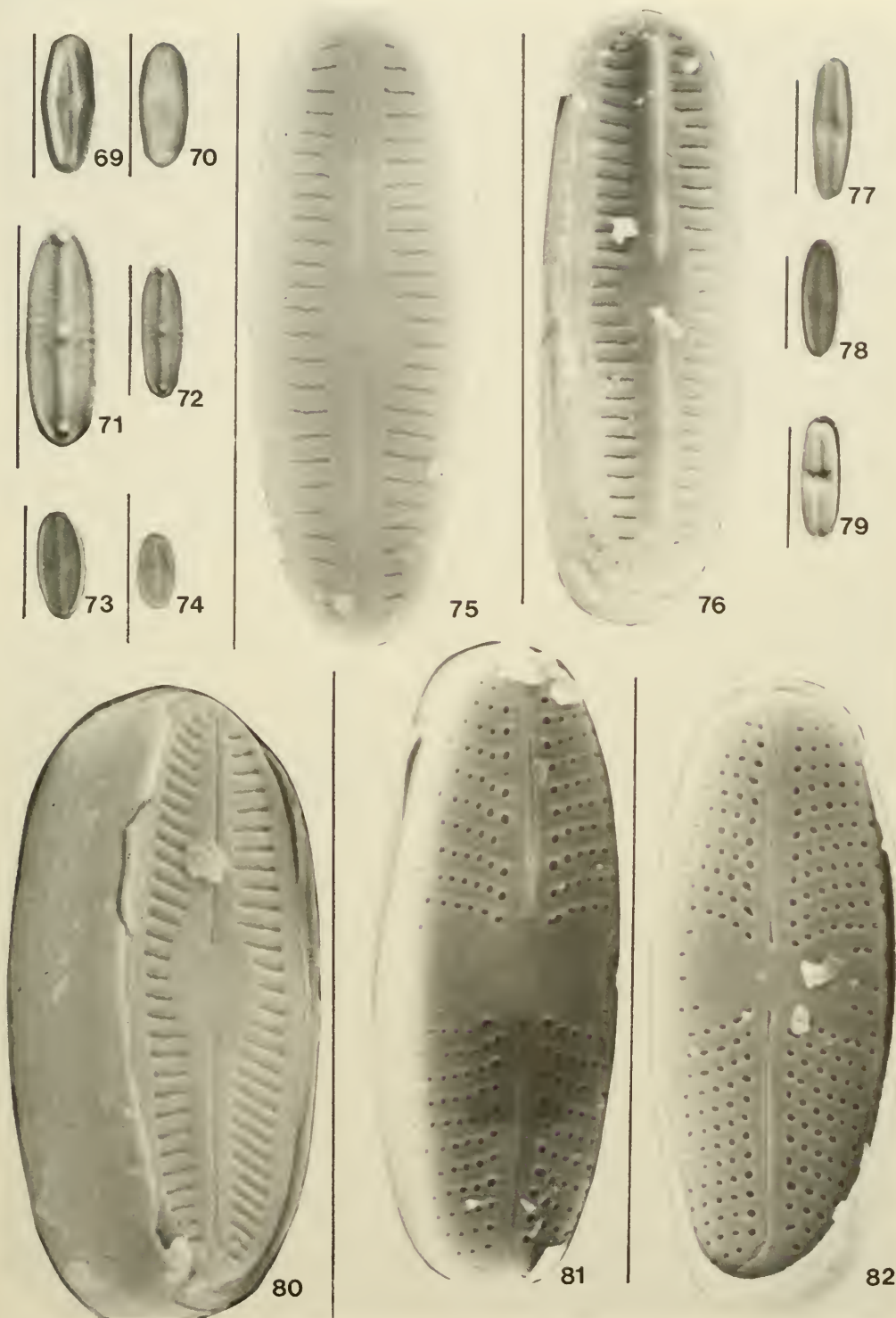
Nitzschia paleacea Grunow (Figs. 96–97). Length 23–38 μm ; width 2–4 μm ; fibulae 9–10 in 10 μm ; striae unresolved (Hustedt 1930:416). Collected only from the passageway between the Throne Room and Neptune's Grotto (Site 5).

DISCUSSION

Distribution and relative abundance data for all diatom species collected are summarized in Table 2. Distribution of species in



Figs. 55-68. *Navicula* spp.: 55-56, *N. brekkaensis* valve views, light micrographs; 57, *N. brekkaensis* valve view, SEM; 58, *N. pupula* var. *rectangularis* valve view, light micrograph; 59-61, *N. cryptocephala* var. *veneta* valve views, light micrographs; 62-65, *N. contenta* f. *biceps* valve views, light micrographs; 66, 68, *N. contenta* f. *biceps* valve views, SEM; 67, *N. contenta* f. *biceps* oblique view of two frustules, SEM. All scales equal to 10 μ m.



Figs. 69-82. *Navicula* spp.: 69-70, *N. perpusilla* valve views, light micrographs; 71-72, *N. minima* valve views, light micrographs; 73-74, *N. pelliculosa* valve views, light micrographs; 75-76, *N. perpusilla* valve views, SEM; 77-79, *N. secura* valve views, light micrographs; 80, *N. pelliculosa* oblique valve view, SEM; 81-82, *N. secura* valve views, SEM. All scales equal to 10 μ m.

the Oregon Caves system is apparently determined by several factors, especially moisture, light, availability of mineral nutrients, and proximity of sites to cave openings. The accumulation of algal material is most prolific in areas immediately adjacent to incandescent light fixtures. Formations highlighted with incandescent lights and having significant amounts of moisture seepage demonstrate a well-developed algal community.

Dry sites (such as sites 1, 6, 7, 8, and 12) were relatively low in species diversity, with an average of 5 species per site. Sites 2, 3, 4, 5, 10, and 11, where moisture accumulation and seepage is continuous, had an average of 11.7 species per site. Generally, those species that occurred at dry sites were ubiquitous and occurred throughout the system. Besides being wet, sites 2, 3, 4, 5, 10, and 11 are all located in close proximity to one of three

cave openings, the entrance, the 110 exit, or the principal exit. Thus, elevated moisture and the close proximity of openings in the cave increase the diversity of diatom species. Sites 1 and 12 are the entrance and main exit to the cave, respectively. Both these sites are in effect exterior to the cave proper and, consequently, the flora at these sites is different from the characteristic cave flora. Several environmental factors vary significantly at these two sites, including no direct exposure to incandescent light, reduced moisture, and seasonal temperature and light fluctuations.

Diversity of species was low at several of the sites, but the actual number of organisms was high for all sites. This is likely attributable to the relatively consistent environmental conditions and daily exposure to incandescent lights throughout the year.

TABLE 2. Diatom distribution in the Oregon Caves National Monument. A = abundant, C = common, R = rare.

	Site 1	Site 2	Site 3	Site 4	Site 5
	Entrance	Between Watson's Grotto Gardens	Passageway of the Whale	110 exit	Passageway between Throne Room and Neptune's Grotto
<i>Melosira roescana</i>		R		R	
<i>Fragilaria construens</i>		R			C
<i>Achnanthes coarctata</i>					
<i>Achnanthes exigua</i>		C	C	C	A
<i>Achnanthes exigua</i> var. <i>heterovalva</i>			A		A
<i>Achnanthes lanceolata</i>		R	R	R	C-A
<i>Achnanthes microcephala</i>			R		
<i>Achnanthes minutissima</i>	C	C	C	C	C
<i>Achnanthes montana</i>		C	C-A	R-C	C
<i>Diploneis oblongella</i>					
<i>Navicula brekkaensis</i>					R
<i>Navicula contenta</i> f. <i>biceps</i>	C	A	R-C	C	
<i>Navicula cryptocephala</i> var. <i>veneta</i>					
<i>Navicula gallica</i> var. <i>montana</i>	A	A	C	C	R-C
<i>Navicula insociabilis</i>		R-C		R	
<i>Navicula minima</i>		R		R	
<i>Navicula pelliculosa</i>			R		
<i>Navicula perpusilla</i>	R-C	C		R	
<i>Navicula pupula</i> var. <i>rectangularis</i>					
<i>Navicula segura</i>	C	C	C	A	C
<i>Pinnularia</i> sp.					R
<i>Cymbella minuta</i> var. <i>silesiaca</i>		R			
<i>Amphora perpusilla</i>					R
<i>Hantzschia amphioxys</i>					
<i>Nitzschia linearis</i>					
<i>Nitzschia paleacea</i>					R
Total species per site	5	13	10	11	12

Diatom species tend to aggregate around light fixtures, particularly in areas where there is a significant buildup of soil or a mat of moss gametophytes. Diatoms generally did not occur on CaCO₃ formations unless there was a substantial accumulation of soil or organic debris. Contrary to the above-mentioned observation, associations of green and blue green algae on CaCO₃ formations were common. This feature of diatom substrate preference is likely related to the paucity of certain mineral nutrients on the CaCO₃ substrates.

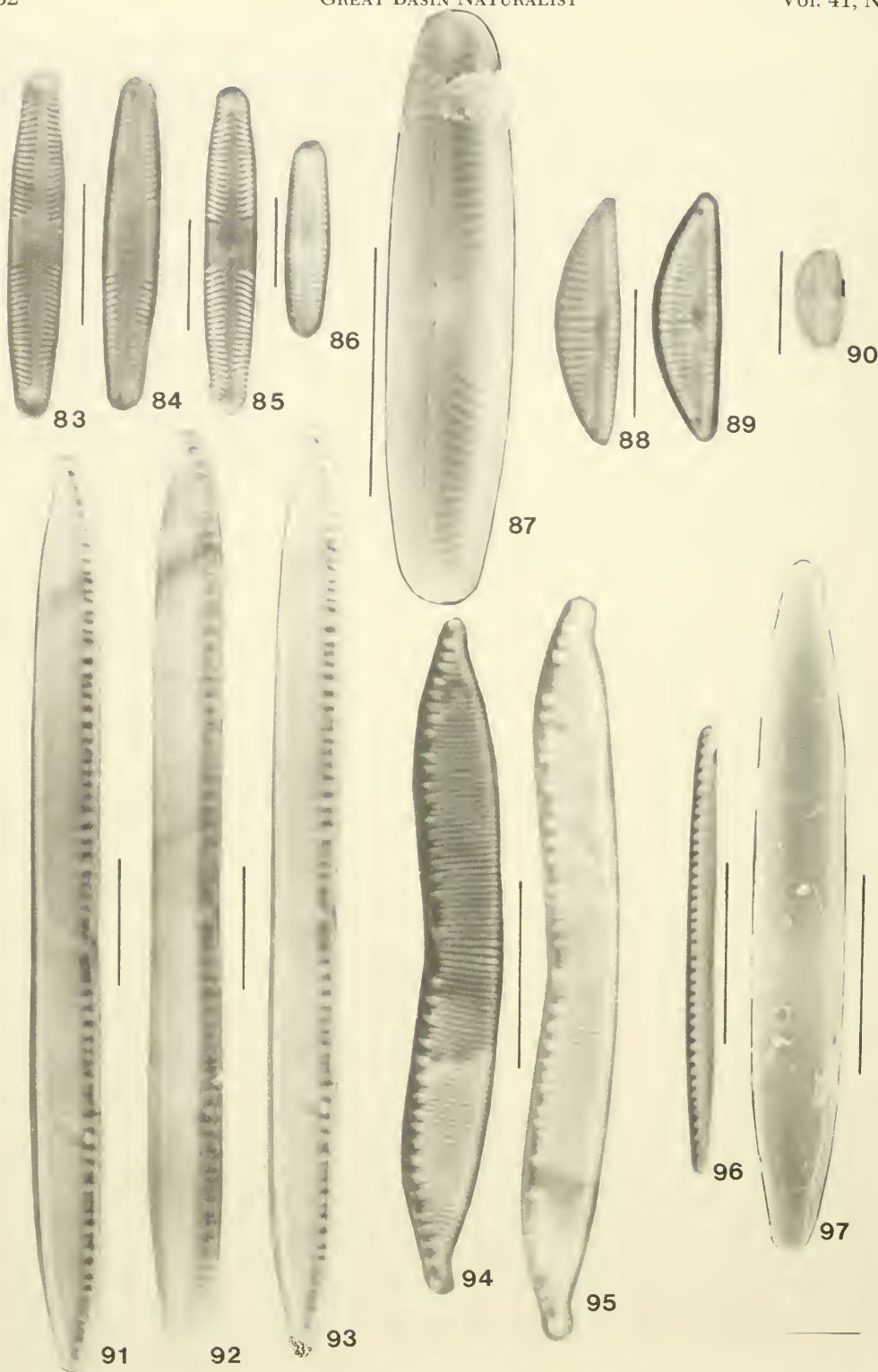
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Table 2 continued.

Site 6	Site 7	Site 8	Site 9	Site 10	Site 11	Site 12
Touching Post	Rhinestone Room	Ghost Room	Slime on stair rail	Wedding Cake Room	Exit tunnel	Face of exit
				R	A	A
	C	R		C	C	R
	C			R	R	
				R-C	R	
C	R	R-C		C	C	
	R			A	C	
R-C		R			C	A
				C		
C	A	C		A	A	R
				R	R	
R-C						
R-C						R
				C-A	C	
				R		
				R	R	
				R		
5	5	4	0	13	12	5



Figs. 83-97. Diatom spp.: 83-86, *Pinnularia* sp. valve views, light micrographs; 87, *Pinnularia* sp. oblique valve view, SEM; 88-89, *Cymbella minuta* var. *silesiaca* valve views, light micrographs; 90, *Amphora perpusilla* valve view, light micrograph; 91-93, *Nitzschia linearis* valve views, light micrographs; 94-95, *Hantzschia amphioxys* valve views, light micrographs; 96, *Nitzschia paleacea* valve view, light micrograph; 97, *Nitzschia paleacea* valve view, SEM. All scales equal to 10 μ m.

ADDITIONAL RECORDS OF THE DARK KANGAROO MOUSE
(*MICRODIPODOPS MEGACEPHALUS NASUTUS*),
WITH A NEW MAXIMUM ALTITUDE

Harold J. Egoscue¹

ABSTRACT.— Three specimens of *Microdipodops megacephalus nasutus* were captured in the Wassuk Mountains of western Mineral County, Nevada, which provide a second place of occurrence for the subspecies and a new altitudinal record of 2455 m for the genus. This is the first time this species has been found in the pinyon-juniper belt.

Records of *Microdipodops megacephalus nasutus* Hall have not been published since the taxon was named (Hall 1941) from six specimens collected at Fletcher, Mineral County, Nevada.

On 10 and 11 September 1980, I collected three specimens referable to *M. m. nasutus* about 600 m northeast of Lucky Boy Pass summit, at a place 19.3 km south of the summit of Mt. Grant (Wassuk Range) and 16.1 km southwest of Hawthorne, Mineral County, Nevada, elevation about 2455 m (8050 ft). These records provide a second place of occurrence for the subspecies and a maximum known elevation for the genus.

The mice were trapped in a small, dry basin, where the primary vegetation was a mixture of big sagebrush, *Artemisia tridentata*, and pinyon pine, *Pinus monophylla*, with an occasional Utah juniper, *Juniperus osteosperma*. Other plants were bitterbrush, *Purshia tridentata*, rabbitbrush, *Chrysothamnus* sp., at least three species of *Eriogonum*, and two of *Phlox*. Grasses were sparse and consisted mostly of rice grass, *Oryzopsis* sp., and an unidentified bunchgrass. The sagebrush averaged about 72 cm tall and had thick trunks in relationship to height that often characterizes this shrub when it has been overbrowsed. The light tan soil was made up of coarse sand and fine gravel that apparently originated from extensive ledges of granitelike material nearby.

Other small mammals captured here were the sagebrush vole, *Lagurus curtatus curtatus*

and deer mouse, *Peromyscus maniculatus sonoriensis*. The association of *Lagurus* and *Microdipodops* is unusual; E. R. Hall (pers. comm.) informed me that he had never caught these species together.

The kangaroo mice were an adult male, a subadult female, and a juvenile female. Standard body measurements of the male were: 143, 74, 25, 9. This individual is appreciably smaller in both total length and length of tail than topotypes of *M. m. nasutus* (Hall 1941), but agrees in color, lack of supraorbital patches, amount of black on the distal part of the tail, and skull characteristics reported for the subspecies. The adult male and subadult female were prepared as specimens and will be deposited in the mammal collection of the University of Utah, Salt Lake City.

Although the extension of range is not great in distance, this is the first locality on the east side of the main mountain range of western Mineral County, where the dark kangaroo mouse has been found and suggests that the species may be more widely distributed in this part of Nevada than supposed.

According to Hall (1946), the altitudinal limits of *Microdipodops megacephalus* are 1189.5–2318 m (av. about 1677.5 m). Of 100 locations where the mice were recorded in Nevada, only one is over 2135 m (7000 ft). Zonally, Hall's localities are Upper and Lower Sonoran, mostly the former. None are in the pinyon-juniper belt.

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ACKNOWLEDGMENTS

Collecting was done under Nevada Department of Wildlife Special License-Permit No. 3385. I thank E. R. Hall for his comments and suggestions.

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GRAZING IMPACTS ON THE SAGEBRUSH COMMUNITIES OF CENTRAL UTAH

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ABSTRACT.— Twenty-three study sites were established in the sagebrush communities bordering Utah Lake. Relic (ungrazed) and grazed stands were represented in the sample. Differences in species composition, vegetation, and soil characteristics were assessed. Major differences in species composition and vegetative characteristics were due to the influence of grazing. Major changes were loss of native perennial grass cover, and increases in cover from introduced annual species. Differences in the soil characteristics were due to habitat rather than grazing influences.

When the pioneers first came into Utah Valley in 1847, they found a vast area of beauty and plenty in which they could successfully build homes, establish farms, and run large herds of sheep, cattle, and horses. Following settlement, grazing and its effects were seen throughout Utah and the West. Through the journals and records of early pioneers and explorers, we are able to confirm the fact that there has been a great deal of vegetation change in the last century and a half, resulting in widespread changes in the communities of sagebrush and other desert vegetation. The lands in which the first pioneers settled contained great quantities of palatable grasses and other forage plants (Cottam 1961, Wakefield 1936). Many settlers owned large herds, and native forage supplies became depleted from the constant grazing and regrazing of the land. This depletion opened the way for increases in such woody plants as sagebrush and juniper, along with other unpalatable species.

In 1877, John D. Lee was taken back to be executed at Mountain Meadows in southern Utah, a once beautiful green valley and favorite resting area for travelers on the Spanish Trail; he was asked to identify the spot on which he had led the dreadful massacre some twenty years before. He could not do it. He was hardly able to recognize the valley at all, describing it as being "God-forsaken" (Birney 1931).

Overgrazing also left its effect on Utah Valley and other valleys in the area. Orson Hyde lamented these occurrences in a General Conference talk 7 October 1865:

I find the longer we live in these valleys that the range is becoming more and more destitute of grass; the grass is not only eaten up by the great amount of stock that feed upon it, but they tramp it out by the very roots; and where grass once grew luxuriantly, there is now nothing but the desert weed, and hardly a spear of grass is seen.

Between here, Temple Square and the mouth of Emigration Canyon, when our brethren, the Pioneers, first landed here in '47, there was an abundance of grass all over these benches; they were covered with it like a meadow. There is now nothing but the desert weed, the sage, the rabbit-bush and such like plants, that make very poor feed for stock (Roberts 1930).

A grazing animal does not eat everything in its path, but it grazes selectively, concentrating on the most palatable and desirable species. This observation of animal behavior and the response of certain plant species to such behavior has led to a classification of plant species with respect to their degree of desirability and degree of value in a grazing community. The first group is classified as decreasers. These are the more palatable species that diminish under prolonged grazing pressure. The second group are increasers, and generally increase under similar use, and are often the less palatable plants in the community. The third group is composed of invaders, plants present only marginally or not at all in native vegetation (e.g., introduced or exotic species); they are usually unpalatable. Under constant grazing use the vegetative composition of the native communities shifts, becoming less and less desirable. As grazing intensity is allowed to increase, the composition may become totally dominated by unpalatable invaders. This condition steadily

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decreases the condition class or value rating of the land (Stoddart 1975).

Even though Utah Valley and its environs are in many localities well studied from the natural history and ecological points of view, little has been reported in the literature with regard to (1) man's impact on the plant communities since settlement, (2) the influence and changes wrought by introduced exotic plants, (3) species composition for the major community types, (4) environmental factors typical of the major community types, and (5) community diversity.

STUDY AREA

Twenty-three study sites were established in plant communities bordering Utah Lake, Utah County, Utah, at approximately 40°10' N, 11°50' W (Fig. 1). Elevations ranged from 1370 m (4500 ft) to 1400 m (4900 ft) above sea level. Study sites were established in grazed and ungrazed areas of the sagebrush community. Study sites were chosen to represent relatively homogeneous vegetation types.

Weather data for Provo, Utah, is representative of the study area. The average annual precipitation is 340 mm (14 inches), with 60 percent of the total falling in the winter and spring months. The hottest month of the year is July, averaging 33 C; the coldest month is January, averaging 3 C. The majority of its runoff water reaches Utah Lake from tributary streams arising in the Uinta and Wasatch mountain ranges directly east of Utah Lake. Precipitation in these mountains ranges from 760 to 1270 mm (30 to 50 inches) annually (Swenson 1972).

MATERIALS AND METHODS

The study sites were selected to depict the range of variation within the sagebrush community in the central Utah area. A 10 × 10 m study plot (0.01 ha) was established at each site. Study plots were delineated by a cord 40 m long with loops every 10 m for corners. The corners were secured by steel stakes. Each plot was subsampled with twenty 0.25 m² quadrats distributed uniformly across the surface of the plot in five rows of four quadrats each.

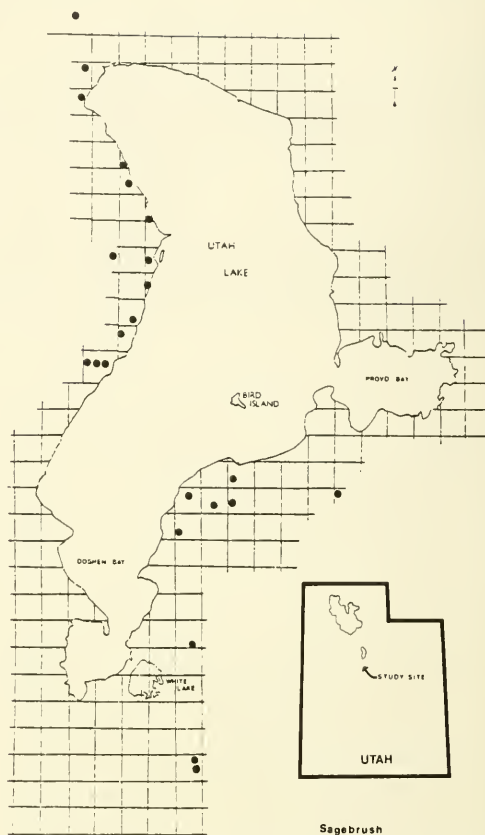


Fig. 1. Map of study site locations in the sagebrush zone in central Utah.

Total living plant cover, plant cover by life form (i.e., shrubs, subshrubs, perennial forbs, perennial grasses, annual grasses, annual forbs, cryptogams), litter, exposed rock, and bare soil were ocularly estimated. Cover for all plant species encountered was also estimated, using the cover class categories (1 = 0 - 5 percent; 2 = 5 - 25 percent; 3 = 25 - 50 percent; 4 = 50 - 75 percent; 5 = 75 - 95 percent; 6 = 95 - 100 percent) suggested by Daubenmire (1959). In addition, all species occurring within the study plot but not encountered in the quadrat subsamples were listed and given a percent cover value of 0.01 so they could be included in the overall data analyses. All species were classified as to life form (see above), longevity (perennial, biennial, annual), and according to whether they are native or introduced.

Three soil samples were taken in each plot (from opposite corners and the center) from the top 20 cm of soil and later combined for

laboratory analysis. This depth was considered adequate because Ludwig (1969), in a study of the different foothill communities in Utah, showed that the surface decimeter of soil when sampled with reference to mineral concentrations yields 80 percent of the information useful in correlations with plant data. Holmgren and Brewster (1972) also showed in a study of desert shrub communities that greater than 50 percent of the fine roots (those most likely to absorb soil minerals) were found concentrated in the upper 15 cm of the soil profile. With respect to grasslands, Christie (1979) found that the top layer of soil is the region of most active mineral uptake.

The following characteristics were recorded for each study plot: elevation (taken from published U.S. Dept. of Interior Geological Survey 7.5 minute series topographic maps); percent slope; slope position (1 = ridgetop, 2 = midslope, 3 = drainage accumulation area); erosion (0 = none, 1 = light, 2 = moderate, 3 = heavy); grazing impact (0 = none, 1 = light, 2 = moderate, 3 = heavy).

Soil samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, mineral composition, and organic matter. Soil reaction was taken with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A 1:1 soil-water paste (Russell 1948) was used to determine pH and total soluble salts. Soils were extracted with 1.0 neutral normal ammonium acetate for calcium, magnesium, potassium, and sodium ions (Jackson 1958, Hesse 1971, Jones 1973). Zinc, manganese, iron, and copper were extracted from the soils by use of DTPA (diethylenetriamine-pentaacetic acid) extracting agent (Lindsay and Norvell 1969). Individual ion concentrations were determined using a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971). Soil phosphorus was extracted by sodium bicarbonate (Olsen et al. 1954). Total nitrogen analysis was made using macro-Kjeldahl procedures (Jackson 1958). Soil organic matter was determined by loss on ignition at 950 C, using a 10-gram sample in a LECO medium temperature resistance furnace following methods described by Allison (1965).

Plant nomenclature follows Welsh and Moore (1973) for the dicotyledons (trees, shrubs, forbs, etc.) and Cronquist et al. (1977) for the monocotyledons (grasses, sedges, rushes, etc.). Prevalent species (those most frequently encountered during sampling) of the various plant communities are reported, with the number being considered equal to the average number of species per 0.01 ha sampling area (Warner and Harper 1972). Diversity values were computed using the formula

$$H^1 = - \sum_i p_i \log p_i,$$

where H^1 is the diversity index and p_i is a measure of the relative abundance of a species in a given habitat (Pielou 1977).

Data taken on the biotic and abiotic factors of the different sites within the study area (one data set per study plot) were lumped by grazing category and summarized. A great deal of variation in the data was observed both within and between categories.

RESULTS AND DISCUSSION

The grazed and ungrazed study sites in the sagebrush communities of central Utah were chosen from established stands surrounding Utah Lake. The grazed sites were chosen from widely spaced areas to represent as nearly as possible the present state of the sagebrush community. The ungrazed sites were chosen to represent stands of the sagebrush community that had not been grazed for the past 35–40 years. Such stands (often classed as “relict areas”) were very difficult to locate.

To successfully assess the effects of grazing on the sagebrush community, prevalent species lists (Table 1) were made for the grazed and ungrazed communities. The number of species considered to be prevalent for each type was calculated by dividing the average number of species per stand by the total number of stands studied. The ungrazed community had 8 prevalent species; the grazed had 10 (Table 2). The greater number of species in the grazed area probably reflected more intense sampling in those areas.

As shown in Table 1, grazing impacts are easily seen in community composition. Decreasers have essentially been eliminated, and the invaders (*Bromus tectorum*, *Ranunculus*

testiculatus, *Poa bulbosa*) have increased in cover from 10 to 59 percent. These are also accompanied by an 18 percent increase in the cover of the woody species *Artemisia tridentata* and *Chrysothamnus nauseosus*. These increases are associated with a reduction in cover (48 percent) of the palatable species (*Agropyron spicatum*, *Poa nevadensis*, *Stipa comata*, *Oryzopsis hymenoides*).

In looking at cover differences in lifeform classes (Table 2), the depletion of grazable vegetation is also evident. The change in shrub cover is due mainly to increases of *Artemisia tridentata*. The corresponding loss of grass cover is due mostly to *Agropyron spicatum*. In addition, the increases in annual forbs and grasses reflect the competitive advantages of unpalatable exotic species (55 percent composition in the grazed area) as palatable species diminish under grazing.

Although one generally expects a reduction of total plant cover after prolonged heavy grazing, in our case the opposite actually proved true. As the way is opened for annuals to invade an area, they spread rapidly and fill in the spaces between and under the shrubs. Thus, in this study, the total living cover increased from 70 to 83 percent under grazing (Table 2). These increases in cover are due to the fact that measurements on total cover were taken in the spring and early summer, when the annuals were at peak growth. By summer and fall they have finished their life cycles and died back, leaving large bare areas of uncovered soil.

The soil studies indicate that grazing had essentially no impact upon the soil texture, hydrogen ion concentration (pH), and chemical nutrients. The higher levels of phosphorus, calcium, sodium, and potassium in the grazed site soils can be accounted for by the fact that the slopes of the two areas were different (ungrazed = 19 percent; grazed = 8 percent); these nutrients are fairly mobile in high calcium content soils and, therefore, as it rains, they tend to be dissolved in runoff water or be carried downhill as absorbed ions on eroded colloidal material.

In addition to results showing modification of vegetation under grazing, another factor affects the chances for the native plants to return. *Ranunculus testiculatus*, a species suspected of allelopathy (Buchanan et al. 1978), deposits harmful chemicals into the soils, causing a retardation of seed germination or complete quelling of the growth of other species. Should these plants cover enough of an area, the native vegetation may never recover.

Grazing has been practiced on most of the plant communities of Utah Valley for many years. As discussed above, its effects can greatly change the structure of the dominant vegetation. The effects documented in the sagebrush communities can also be observed in the shadscale and greasewood communities. Although data are unavailable, the effects are highly similar and in some areas large stands of these types have been denuded of perennial vegetation and are now classified as mixed weed communities.

TABLE 1. Means and standard deviations (SD) of plant species cover on grazed and ungrazed sites around Utah Lake.

Prevalent species	Grazed		Ungrazed	
	Mean	SD	Mean	SD
<i>Artemisia tridentata</i>	31.2	9.3	18.3	9.4
<i>Bromus tectorum</i>	30.9	18.9	9.9	12.3
<i>Agropyron spicatum</i>	0.1	0.5	29.9	24.0
<i>Ranunculus testiculatus</i>	26.2	15.6	0.3	0.6
<i>Poa nevadensis</i>	4.8	7.5	15.4	15.4
<i>Xanthocephalum sarothrae</i>	1.1	1.7	6.8	10.4
<i>Stipa comata</i>	—	—	5.4	13.2
<i>Alyssum alyssoides</i>	1.3	2.2	4.2	6.8
<i>Phlox longifolia</i>	3.4	13.6	0.9	2.1
<i>Chrysothamnus nauseosus</i>	2.8	8.5	1.0	2.3
<i>Sitanion hystrix</i>	2.3	3.3	—	—
<i>Sphaeralcea coccinea</i>	2.2	4.0	0.5	1.2
<i>Poa bulbosa</i>	2.0	8.4	—	—
<i>Poa sandbergii</i>	1.8	5.1	—	—
<i>Oryzopsis hymenoides</i>	—	—	1.8	4.3

TABLE 2. Means and standard deviations of environmental factors and significance levels for the difference of the means for grazed and ungrazed sites around Utah Lake. Significance levels were computed using the student t-statistic.

Environmental factor	Grazed		Ungrazed		Significance level
	Mean	SD	Mean	SD	
GENERAL SITE FACTORS					
Elevation (feet)	4624.0	108.2	5472.0	894.7	.05
Percent slope	8.3	8.2	19.2	14.3	NS
Slope position ^a	2.1	0.8	2.2	0.8	NS
Moisture index ^b	1.1	0.6	1.2	0.4	NS
Erosion index ^c	0.2	0.4	0.0	0.0	.05
Percent litter cover	6.9	4.8	5.6	3.0	NS
Percent exposed rock	2.7	2.7	13.7	14.1	NS
Percent exposed bareground	9.1	5.2	11.2	5.1	NS
GENERAL SOIL FACTORS					
Percent sand	40.7	10.2	32.0	6.7	.05
Percent silt	37.4	6.6	44.0	5.4	.05
Percent clay	22.2	4.4	24.0	2.8	NS
Percent fines	56.6	9.8	68.0	6.7	.05
Percent organic matter	2.3	0.8	3.0	0.5	0.05
pH	7.4	0.2	7.5	0.1	NS
Soluble salts (ppm)	293.7	38.3	275.2	36.8	NS
SOIL MINERAL NUTRIENTS					
Nitrogen (percent)	0.1	0.1	0.2	0.1	NS
Phosphorus (ppm)	11.2	3.9	6.1	2.0	.05
Calcium (ppm)	7500.2	2139.4	6258.3	2960.6	NS
Magnesium (ppm)	227.3	69.1	229.7	100.1	NS
Sodium (ppm)	176.9	53.9	62.6	7.6	.05
Potassium (ppm)	566.6	225.7	305.3	78.4	.05
Iron (ppm)	5.2	2.5	6.2	1.5	NS
Manganese (ppm)	9.4	3.5	9.7	3.8	NS
Zinc (ppm)	1.5	0.7	1.5	1.3	NS
Copper (ppm)	1.9	0.6	1.7	0.7	NS
BIOTIC FACTORS					
Total living cover	83.1	6.6	69.9	10.9	NS
Percent shrub cover	29.1	8.2	26.6	10.5	NS
Percent forb cover	3.8	7.6	1.5	2.9	NS
Percent grass cover	9.9	9.8	51.3	11.6	.05
Percent annual cover	43.0	27.1	11.3	14.6	.05
Percent annual grass cover	22.2	15.3	8.4	10.6	.05
Percent annual forb cover	20.8	11.8	2.9	3.9	.05
Percent cryptogam cover	14.9	12.2	9.4	8.4	NS
Diversity ^d	2.2	0.3	2.0	0.5	NS
Mean no. of species/stand	10.0	3.1	7.8	3.3	NS
Mean no. of native species/stand	6.3	2.7	6.5	2.6	NS
Mean no. of introduced species/stand	3.8	0.8	1.3	1.0	.05
Native species (percent of total)	60.8	8.8	83.5	9.5	.05
Introduced species (percent of total)	39.3	8.8	16.5	9.5	.05
Total cover of native species	43.2	14.5	87.2	13.4	.05
Total cover of introduced species	56.8	14.5	12.8	13.4	.05
Grazing impact ^e	2.2	1.2	0.5	0.6	.05

^aSlope position is defined as 1 = top of slope, 2 = midslope, 3 = bottom of slope.
^bThe moisture index runs from 1 to 5 with 1 indicating xeric conditions and 5 indicating standing water.
^cThe erosion index runs from 0 to 3 with 0 indicating no erosion and 3 indicating heavy erosion.
^dDiversity was computed using Shannon-Weiner's index.
^eGrazing impact is defined as 1 = light, 2 = moderate, and 3 = heavy grazing.

Grazing effects in the meadows have been less dramatic because of more favorable moisture conditions and because of the general capacity of the dominant life forms (i.e., grasses and sedges) to withstand grazing pressure. Changes due to grazing pressures in the native vegetation of these areas most often take the form of shifts in the dominance of species over long periods (i.e., as more palatable species are grazed in preference to others, the competitive ability of grazed species is reduced, thus allowing the less palatable species to increase in dominance). Such changes are difficult to document because of the long time periods needed to make the shifts and because of the lack of "relict" meadows for comparison purposes.

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ADAPTING SALT CREEK PUPFISH (*CYPRINODON SALINUS*) TO FRESH WATER

Thomas M. Baugh¹

ABSTRACT.—The Salt Creek pupfish, *Cyprinodon salinus*, is adapted to fresh water in aquaria.

The Salt Creek pupfish, *Cyprinodon salinus* is endemic to Salt Creek, a short, 2 km, spring-fed stream located at about 70 m below sea level on the floor of Death Valley, Inyo County, California. Although this cyprinodont was first described as a separate species by Miller (1943), it appears only infrequently in the subsequent literature (Burley 1978, Brown and Feldmeth 1971, Hunt 1975, LaBounty and Deacon 1972, Miller 1948, Miller 1968, Soltz and Naiman 1978).

To obtain specimens for a study of social behavior, twelve *C. salinus* were taken from Salt Creek on 30 September 1980. The fish, which ranged in size from 15 to 35 mm, were captured with dip nets from open waters near the banks of the first small pool below McLean Spring and from a mud-detritus substrate at the same pool. Water temperature at the time of capture was 17.8 C, and salinity of the water was 20 o/oo. The fish were placed in stream water in a 7.6 liter plastic bucket and transported by backpack, automobile, and airline to the laboratory, where they were placed in a 75 liter aquarium on 2 October 1980.

The water in the aquarium consisted of aged (21 days) tapwater to which had been added enough Instant Ocean[®] synthetic salts to bring the salinity to 20.6 o/oo. The fish accepted a mixed diet of TetraMin Staple Food[®], Tetra Krillflakes[®], and Tetra AlgaeFlakes[®] at 0600 and San Francisco Bay Brand[®] frozen brine shrimp at 1630.

To circumvent problems associated with maintaining fish in saline aquarium environments, I decided to desalinate *C. salinus* and conduct behavioral observations in a freshwater environment. Stuenkel and Hillyard (1978) reported maintaining this species in

freshwater but gave no details or schedule for desalination.

Desalination began on 4 October by the removal of saline aquarium water and the addition of an equal amount of aged (7 days) tapwater. During the desalination sequence, starting from a salinity of 20.6 o/oo, daily salinity was as follows: 17.8, 15.3, 12.7, 10.1, 7.5, 4.8, and 3.4. Throughout this schedule the water temperature was maintained at 20 C.

After six months the fish have shown no adverse effects to the adaptive procedure. In addition, they have spawned repeatedly in this freshwater environment.

ACKNOWLEDGMENTS

I thank George Von derLippe, superintendent, and Peter G. Sanchez, resource specialist, Death Valley National Monument, for their help in various phases of my work with this species.

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WINTER CRUDE PROTEIN AMONG ACCESSIONS OF FOURWING SALTBUSH GROWN IN A UNIFORM GARDEN

Bruce L. Welch¹ and Stephen B. Monsen²

ABSTRACT.— Winter crude protein content was determined for the current year's growth of 43 accessions of fourwing saltbush (*Atriplex canescens*) grown on a uniform garden. The crude protein level varied among accessions from 6 percent to 14 percent of dry matter. Individual plants (215) ranged from 5.3 percent to 17.1 percent. The mean winter crude protein level was 9.6 percent. Because these data were generated on even-aged plants, it appears that genetic variation plays an important role in determining the level of crude protein in fourwing saltbush.

Protein is one of three nutrients commonly listed as being deficient in the winter diet of mule deer and livestock on native ranges (Dietz 1965, Halls 1970, Nagy and Wallmo 1971, Welch and McArthur 1979a). Plants that retain significant amounts of green leaves during the winter usually contain higher levels of crude protein than those that shed their leaves (Ensminger and Olentine 1978, Monsen et al. [in preparation³]). There is some indication that individual plants and accessions of fourwing saltbush (*Atriplex canescens*) vary in the number of leaves retained during the winter (Plummer et al. 1966, McArthur et al. 1978). This differential retention of winter leaves among individual plants and accessions of fourwing saltbush is probably associated with differences in winter crude protein content (Monsen et al. [in preparation³]). We, therefore, undertook this study to determine if some accessions of fourwing saltbush grown on a uniform garden produce significantly higher levels of crude protein than others.

MATERIALS AND METHODS

A uniform garden was located about 8 km south of Bliss, Idaho. Prior to planting, the garden was cleared of Wyoming big sagebrush, *Artemisia tridentata* ssp. *wyomingensis*, and associated perennials and annual grasses. Cultural methods were used to control the weeds.

Fourwing saltbush seed was collected from 60 native stands in eight states (Table 1). The seeds were stratified and then planted in small containers for the production of containerized stock. Following germination, the seedlings were grown in a greenhouse for approximately 10 weeks. The seedlings were then hardened off and planted in the garden during the spring of 1977. For each accession, 20 plants were planted on a 2.5 m grid within each of four plots in the garden.

From this garden, 43 accessions of fourwing saltbush were selected from one plot to evaluate the variation of winter crude protein levels. Table 1 lists the county and state where the seeds for each accession were collected. From each accession, 5 plants were selected at random for this study. Current year's growth was collected at random throughout the entire crown of the plants. Samples were placed in paper bags and transported to the laboratory and allowed to air dry for 5 days. Then, the samples were ground in a Wiley mill and passed through a 1 mm screen and oven dried at 100 C for 48 hours. Total nitrogen was determined by the Kjeldahl method as outlined by the Association of Official Analytical Chemists (1980). Crude protein was calculated by multiplying the nitrogen content by 6.25 (Association of Official Analytical Chemists 1980). Data were expressed on a percent of dry matter basis.

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³Monsen, Stephen B., Bruce L. Welch, and Nancy L. Shaw. Winter leafiness and crude protein content of antelope bitterbrush, desert bitterbrush, cliffrose, and Apache-plume accessions grown in a uniform garden. In preparation.

A completely random analysis of variance ($P = .01$) was used to detect significance among the 43 fourwing saltbush accessions. Hartley's test ($P = .05$) was used to test for significant differences among accession means. Percentages were transformed to Arcsin to avoid inequalities (Snedecor and Cochran 1967).

RESULTS AND DISCUSSION

The crude protein levels of the 43 accessions ranged from 6.0 to 14.2 percent with a

TABLE 1. Location of fourwing saltbush seed collection areas by county and state. Names given in parentheses are either towns or geographic features near the collection site.

1. Juab County, Utah (Jericho)
2. Kane County, Utah (Kanab)
3. Washoe County, Nevada (Reno Experiment Station)
4. Emery County, Utah (Hiawatha)
5. San Juan County, Utah (Monticello)
6. Owyhee County, Idaho (Reynolds Creek)
7. Lincoln County, Nevada (Panaca)
8. Sanpete County, Utah (Fayette)
9. San Juan County, Utah
10. Iron County, Utah (Lund)
11. Delta County, Colorado (Delta)
12. Unknown, Arizona (Little Colorado)
13. Navajo County, Arizona (Keams Canyon)
14. Rio Arriba County, New Mexico
15. Millard County, Utah (Garrison)
16. Sweetwater County, Wyoming (Green River)
17. Rio Arriba County, New Mexico (Rincon Blanca)
18. Emery County, Utah (Huntington)
19. Juab County, Utah (Nephi)
20. Coconino County, Arizona (Kaibab National Forest)
21. Emery County, Utah (San Rafael Swell)
22. Juab County, Utah (Excel Canyon)
23. Mesa County, Colorado (Grand Junction)
24. Garfield County, Utah (Escalante)
25. Iron County, Utah (Cedar City)
26. Elmore County, Idaho (Bliss)
27. Washington County, Utah (St. George)
28. Uintah County, Utah (Manila)
29. Carbon County, Utah (Ivy Creek)
30. Beaver County, Utah (Milford)
31. Sanpete County, Utah (Ephraim)
32. Wasatch County, Utah (Timpanogos)
33. Millard County, Utah (Desert Range Experiment Station)
34. Washington County, Utah (Pine Valley)
35. Gunnison County, Colorado (Gunnison)
36. San Juan County, Utah (Fry Canyon)
37. Juab County, Utah (Tintic Valley)
38. San Juan County, Utah (Mexican Hat)
39. Emery County, Utah (Emery)
40. Coconino County, Arizona (Tuba City)
41. Uintah County, Utah (Randlett)
42. Bighorn County, Montana (Decker)
43. Washington County, Utah (Jackson Springs)

mean of 9.6 percent (Table 2). The crude protein of individual plants (215) ranged from 5.3 to 17.1 percent.

These crude protein values compare to big sagebrush 12.4 percent (Welch and McArthur 1979a, 1979b), curleaf mahogany 10.3 percent (Smith 1952, Austin and Urness 1980), chokecherry 9.9 percent (Smith 1957), desert bitterbrush 9.0 percent (Monsen et al. [in preparation³]), Stansbury cliffrose 8.6 percent (Smith 1957, Monsen et al. [in preparation³]), antelope bitterbrush 7.8 percent (Smith 1952, Bissell et al. 1955, Dietz et al. 1962, Monsen et al. [in preparation³]), and dormant grass 3.7 percent (National Academy of Science 1964).

Analysis of variance detected significance ($P = .01$) due to accession (Table 2). Hartley's test detected that some accessions contained significantly higher levels of winter crude protein than others. Accessions from Washington County, Utah (Jackson Springs); Bighorn County, Montana (Decker); and Uintah County, Utah (Randlett) contained the highest winter crude protein among the 43 accessions tested. Accessions collected from Juab County, Utah (Jericho); Kane County, Utah (Kanab); and Washoe County, Nevada (Reno Experiment Station) contained the least amount of winter crude protein. There was significant variation among plants within a given accession. This is illustrated in Table 2 by the accessional coefficients of variation. The coefficients of variation for the 43 accessions ranged from a low of 3.4 percent to a high of 33.9 percent. The mean coefficient of variation was 17.2 percent. For those accessions with a large amount of variation, careful intra-accessional selection could greatly improve the winter crude protein levels of these accessions.

There is some evidence that accessions of fourwing saltbush growing in a uniform garden may vary in other important characteristics, such as palatability, productivity, and adaptability (Van Epps and McKell 1978, McArthur et al. [in preparation⁴]). Our main objective in the selection and breeding of

⁴McArthur, E. Durant, A. Clyde Blauer, and Richard Stevens. Differential adaptation and production among accessions of fourwing saltbush grown on uniform gardens. In preparation.

TABLE 2. Hartley's test of winter level of crude protein (percent dry matter) among 43 accessions of fourwing saltbush* (*Atriplex canescens*). Five plants per accession. Also accessional coefficient of variation is given.

Accession number	Percent crude protein	C.V.
1	6.0**	14.0***
2	7.1	17.3
3	7.5	11.4
4	7.6	16.0
5	7.7	7.1
6	7.7	9.9
7	7.8	16.4
8	7.9	19.9
9	8.0	18.5
10	8.0	24.1
11	8.1	8.4
12	8.1	12.3
13	8.2	3.4
14	8.3	15.9
15	8.3	14.2
16	8.6	23.5
17	8.7	33.9
18	8.9	24.1
19	9.0	31.5
20	9.1	16.3
21	9.2	14.7
22	9.2	7.2
23	9.3	9.9
24	9.3	10.4
25	9.5	20.8
26	9.6	5.9
27	9.8	29.7
28	9.8	18.7
29	10.0	8.3
30	10.2	28.1
31	10.2	23.7
32	10.4	14.2
33	10.6	13.9
34	10.9	28.4
35	11.5	22.8
36	11.7	10.3
37	11.9	16.7
38	12.0	25.5
39	12.2	22.7
40	12.9	27.8
41	13.8	11.2
42	14.1	21.5
43	14.2	10.8

*For location of accession see Table 1.
**Accessions sharing the same line are not significantly different at the 95 percent level.
***C.V. = Coefficient of variation—five replications per accession.

fourwing saltbush will be to combine high protein content with other desirable characteristics that will provide more nutrients for wintering big game and livestock.

ACKNOWLEDGMENTS

We thank Kathleen Mitterholzer and Nancy Shaw for their technical assistance. Seeds

were provided by the Utah Division of Wildlife Resources through the Pittman-Robertson Project, W-82-R, located at Ephraim, Utah.

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COYOTE-BADGER ASSOCIATIONS

Philip N. Lehner¹

ABSTRACT.— Four observations made in Jackson Hole, Wyoming, indicate that coyote-badger associations are best considered as phoretic (accidental and nonobligatory) rather than a form of social symbiosis as has been previously suggested.

Occasional reports of coyote-badger associations generally consider them (explicitly or implicitly) to be some form of social symbiosis ranging from commensalism to social mutualism. Four observations of coyote-badger associations I made on the National Elk Refuge, Jackson, Wyoming (26 July, 1, 7 and 10 August 1976) prompted me to reconsider previous interpretations of these associations.

Van Wormer (1964) and Rimington (in Seton 1909) imply that the association is a *commensal* relationship in which the coyote benefits by capturing prey missed by the badger without the badger being adversely affected. On one occasion I observed a coyote attending to an apparent ground squirrel hole about 25 m from where a badger was digging at a hole the coyote had left less than one minute before. The coyote suddenly pounced, thrust its muzzle into the hole, then withdrew it and trotted away, apparently unsuccessful in its attempt to capture a ground squirrel. This type of association would be analogous to various species of reef fish accompanying goatfish in order to capture prey that elude the goatfish (Hobson 1968). The badger is, however, not totally unaffected. The coyote occasionally nips the badger (Hill in Dobie 1961, M. Wells pers. comm.), and Rathbun et al. (1980) describe three coyotes killing a half-grown badger. In addition, the coyote sometimes steals prey from the badger (Shoemaker in Dobie et al. 1965, Price in Dobie 1961). This occasional cleptoparasitism is perhaps a natural progression from the capturing of prey missed by the badger. Also,

observations of badgers following coyotes (Robinson and Cummings 1947, Warren 1910) suggest that the badger benefits from the association. During all four of my observations, the badger followed the coyote at least part of the time.

Several observers imply a stronger relationship in the form of *social mutualism* (Cahalane 1950, Dobie 1961, Grinnell in Dobie et al. 1965, Ryden 1975, Young and Jackson 1951). This is supported by observations of the two traveling side-by-side (Suter in Cahalane 1950) and changing leaders. On 26 July 1976 I observed a coyote and badger change leadership several times during the 55 minutes they were in view. The leader often looked back at the follower and paused as if waiting for the other to catch up. A similar observation was made by Robinson and Cummings (1947). In addition, badgers apparently unearth prey chased into burrows by coyotes (Dobie 1961, Dobie et al. 1965). On 10 August 1976 I observed a badger approach a coyote that was lying down near an apparent ground squirrel hole. The badger stuck its muzzle into the hole at which point the coyote arose, walked to another nearby hole and stuck its nose in as if sniffing. The badger immediately ran to that hole and began digging. The coyote then laid down and appeared to watch the badger dig. At one point the coyote leaped up, approached the digging badger, and poised as if ready to pounce on prey. Nevertheless, I observed no prey being caught, and the badger quit digging. It may be that the coyote possesses a superior sense of smell for detecting the presence of ground squirrels (Dobie 1961).

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My observations support the belief that there is a *mutual attraction* between the two species. The widespread occurrence of reported coyote-badger associations (Alberta, Oregon, Montana, North Dakota, South Dakota, Wyoming, Colorado, Texas, New Mexico, and Mexico) suggest an inherent propensity for the association. In addition to associating while hunting, on two occasions I saw them rest together in the same clump of sagebrush. Nevertheless, the association is neither obligatory nor prolonged, conditions necessary for any type of "*true*" *social symbiosis* (Wilson 1975). Rather, this nonobligatory association comes closest to being *phoretic* (Cheng 1970). Whether one (or both) species seeks out the other is not known. Meeting may be somewhat accidental or promoted by their aggregation at a common prey resource. I suggest that coyote-badger associations are initially analogous to the associations that coyotes develop with ravens and magpies (Murie 1940). Continued associations are probably prompted by both individuals learning that food may be obtained (perhaps more efficiently) by the association and enhanced by the coyotes' own social tendencies. For example, badgers have been observed associated with two (Hill in Dobie 1961) and three coyotes (Cortez in Dobie 1961). On 7 August 1976 I observed a badger following two adult coyotes. The badger always trailed behind the larger coyote as it wound its way around clumps of sagebrush. Whether this attachment to a particular individual is common in coyote-badger associations may be determined with additional observations.

ACKNOWLEDGMENTS

I am indebted to Mike Wells for sharing his field notes and for reviewing this manuscript. I also thank Bruce Wunder for his comments on an earlier draft. This study was funded, in part, by a grant from the New York Zoological Society.

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NEW NEARCTIC CHLOROPERLIDAE (PLECOPTERA)

Rebecca F. Surdick¹

ABSTRACT.— *Alloperla furcula*, *A. hamata*, *A. roberti* and *Triznaka spinosa* are described from North America. A new genus, *Bisancora*, based on the new species *B. rutiformis*, is described and includes *B. pastina* (Jewett). *Alloperla quadrata* is synonymized with *A. leonarda* Ricker.

During biosystematic research on Nearctic Chloroperlidae, several new species and a new genus were discovered. *Alloperla quadrata* Harden & Mickel was found to be conspecific with *A. leonarda* Ricker.

Alloperla furcula, sp. nov.
Figs. 1–5

General color beige in alcohol. Antennae pale proximally, darker distal to fifth segment, with dusky basal segment; head unpatterned except for three dark ocellar rings; occiput short with lateral edges tapering immediately posterior to compound eyes. Pronotum squarely oval, dusky laterally, narrower than head by width of compound eyes; mesonotum, metanotum, and abdomen lacking dark markings; cercal segments 7–9; copious setation slightly dusker than integument on legs, pronotum, forewings. Wings macropterous, hyaline, representative of genus.

MALE.— Forewing length 5.5 mm; body length 6.5 mm. Epiproct tip elongate, parallel-sided, fuscous, evenly sclerotized; apex bifurcate with acute prongs directed laterad almost perpendicular to long axis of epiproct tip; lateral aspect thin, tapered to ventrally hirsute apex; base set in enlarged cowl extending anteriorly to bifurcate apex. Basal anchor twice as wide as long; paragenital plates as wide as basal bar. Aedeagus membranous. Lateral brushes on segments 8 and 9.

FEMALE.— Forewing length 6.5 mm; body length 7 mm. Subgenital plate with sides sloping steeply to an acute median projection

one-half length of sternite 8; lateral aspect narrowly conical. Sternite 8, including subgenital plate, evenly hirsute except for a pair of sparsely haired patches on posterior half at base of subgenital plate flanking its swelled axis. Vagina membranous. Lateral brushes on segments 7 through 9.

MATERIAL.— Holotype ♂, allotype, paratypes 22 ♂, 118 ♀: South Carolina, Aiken Co., Upper Three Runs Crk., Savannah River Plant, 17-V-1977, Herlong and Prichard (USNM #76886). 37 ♂, 387 ♀ paratypes: South Carolina, Aiken Co., Upper Three Runs Crk., Savannah River Plant, 1-VI-1977, Herlong and Prichard (B. P. Stark, R. F. Surdick, J. C. Morse, R. W. Baumann).

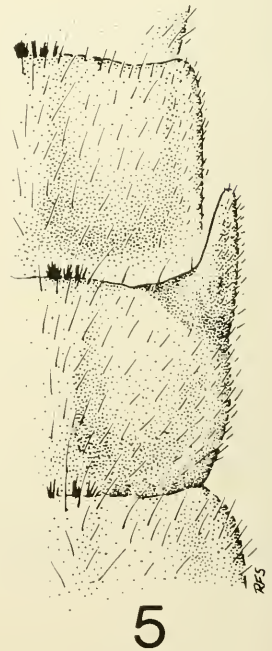
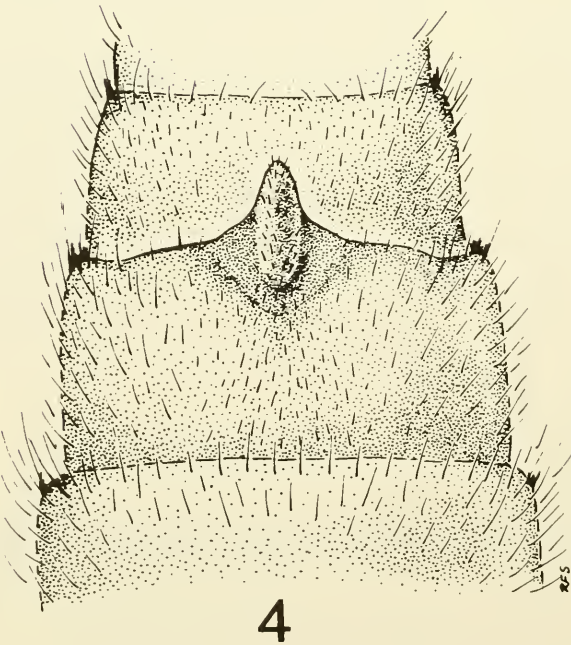
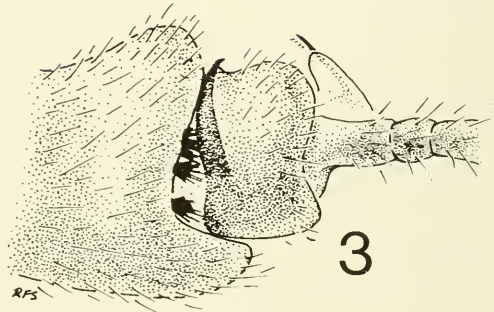
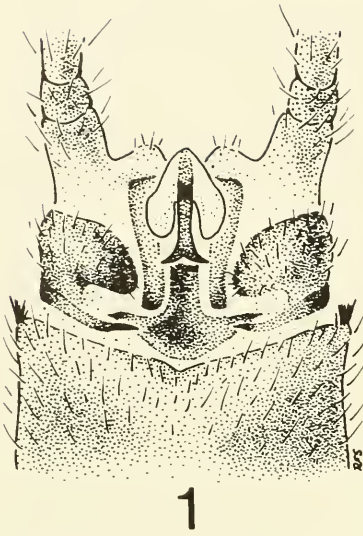
ETYMOLOGY.— The Latin adjective *furcula* refers to the small fork on the apex of the epiproct tip.

DIAGNOSIS.— *Alloperla furcula* differs from other species with similar epiprocts and cowl by the prominence of the apical prongs. *Alloperla natchez* Surdick & Stark bears a thinner, more tapered epiproct tip that has minute lateral extensions on the ventrally bent apex. *Alloperla leonarda* Ricker has small lateral projections on the blunt apex of the epiproct tip. The triangular, posterior projection of the subgenital plate is longer and more acute in *A. furcula* than in either of the other species.

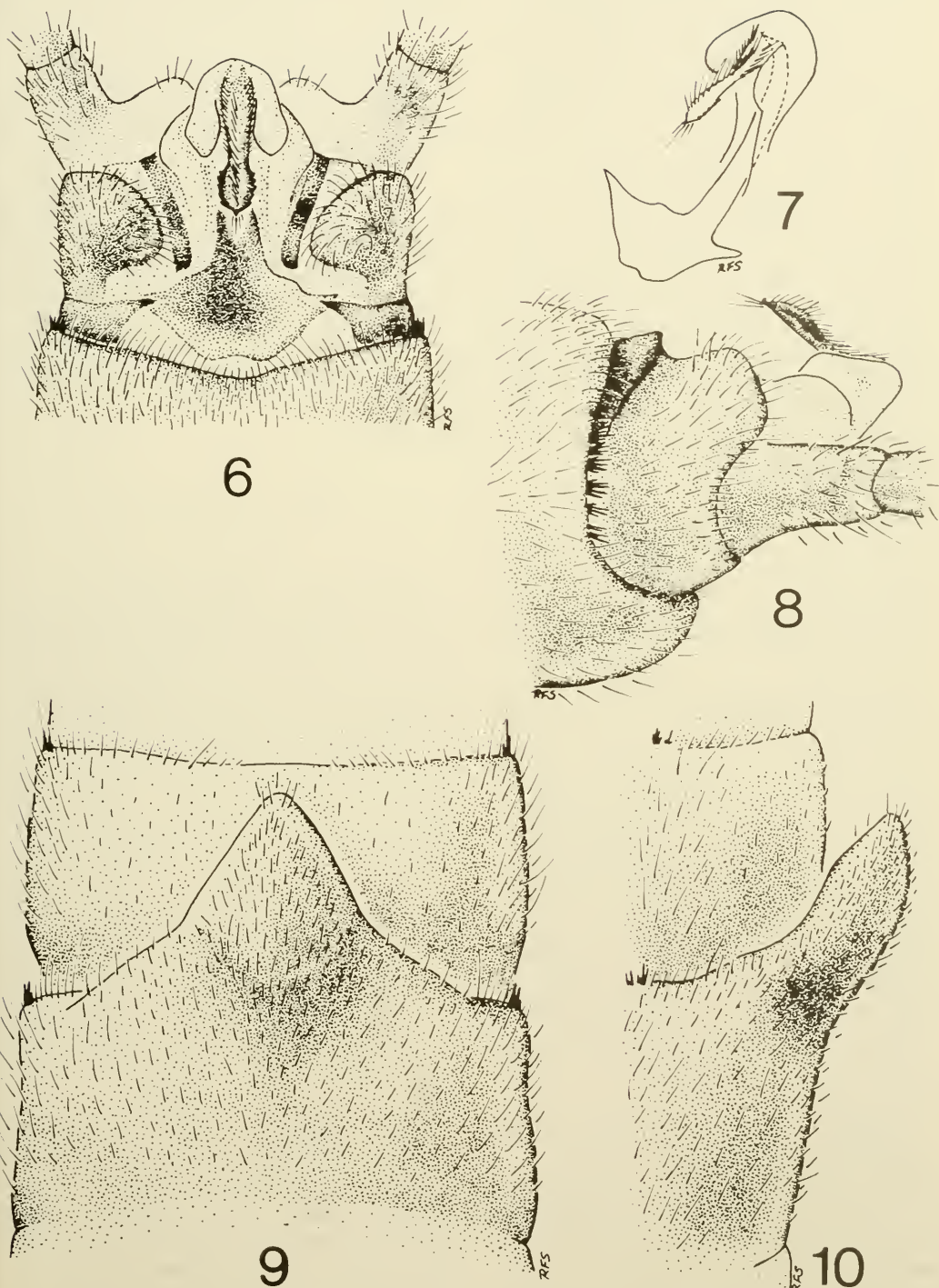
Alloperla hamata, sp. nov.
Figs. 6–10, 16

General color pale yellow in alcohol. Antennae pale; head unpatterned except for three dark ocellar rings; occiput short with

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Figs. 1-5. *Alloperla furcula*: (1) male terminalia, dorsal; (2) epiproct, $\frac{3}{4}$ view; (3) male terminalia, lateral; (4) female terminalia, ventral; (5) female terminalia, lateral.



Figs. 6-10. *Alloperla hamata*: (6) male terminalia, dorsal; (7) epiproct, $\frac{3}{4}$ view; (8) male terminalia, lateral; (9) female terminalia, ventral; (10) female terminalia, lateral.

lateral edges tapering slowly, convexly, posterior to compound eyes. Pronotum squarely oval; narrower than head with indistinct, dusky reticulations; posterior margin twice as wide as anterior. Legs, mesonotum, metanotum, and abdomen lacking dark markings except for dusky sutures; cercal segments 9–10. Wings macropterous, hyaline, representative of genus without reduction in venation.

MALE.—Forewing length 9 mm; body length 8 mm. Epiproct tip elongate; basal two-thirds tapered; distal third swollen to width and thickness of base, with serrate lateral margins and apical upturned tooth; fine long hairs beneath apical tooth, along dorsal medial axis, and along lateral margins of basal tapering section. Cowl not enlarged. Basal anchor 1.5 times as wide as long; paragenital plates thinner than basal bar. Aedeagus membranous. Lateral brushes on segments 7 through 9.

FEMALE.—Forewing length 9–9.5 mm; body length 8.5–9 mm. Subgenital plate as long as sternite 8, extending posteriorly over half of sternite 9; lateral margins concave, with posterior halves forming terminal half of diamond-shaped conical swelling; swelling obvious in lateral aspect, forming half of subgenital plate. Subgenital plate evenly hirsute with longer hairs on margins; sternite 9 with evenly scattered fine hairs. Vagina membranous. Lateral brushes on segments 7 through 9.

MATERIAL.—Holotype ♂, allotype, 1 ♂, 2 ♀ paratypes: Alabama, Jackson Co., intermittent crk. adjacent Ala. Hwy. 65, 8.3 mi. N. jct. Ala. Hwy. 146, 16-IV-1976, A. M. James (USNM #76887). 1 ♂, 3 ♀ paratypes: Alabama, Jackson Co., Francisco, adjacent Ala. Hwy. 65, .7 mi. S. Tenn. stateline, 16-IV-1976, A. M. James (R. F. Surdick).

ETYMOLOGY.—The Latin adjective *hamata* refers to the barb-like appearance of the epiproct tip.

DIAGNOSIS.—*Alloperla hamata* belongs to the species group including *A. banksi* Frison (Fig. 15) and *A. imbecilla* (Say) (Fig. 14). Most similar to the former, it is distinguished by the thinness and increased taper of the epiproct tip. *A. hamata*, however, bears a thicker and less tapered epiproct tip than *A. imbecilla*. Females of all three species are similar. *Alloperla hamata* probably represents

the southernmost isolate of a far-ranging species ancestral to the *Alloperla imbecilla* group.

Alloperla leonarda Ricker

Alloperla leonarda Ricker, 1952: 176, figs. 132, 135.

Alloperla quadrata Harden & Mickel, 1952: 61, pl. X, fig. 6. *New synonymy*

Comparison of the female holotype of *Alloperla quadrata* Harden & Mickel with the female allotype and specimens of *Alloperla leonarda* Ricker indicated synonymy of the two species. The abbreviated subgenital plate of *A. quadrata* appears to be within the genetic variation and physical distortion of *A. leonarda*. *Alloperla quadrata* was also collected within the geographic range of *A. leonarda*.

Alloperla roberti, sp. nov.

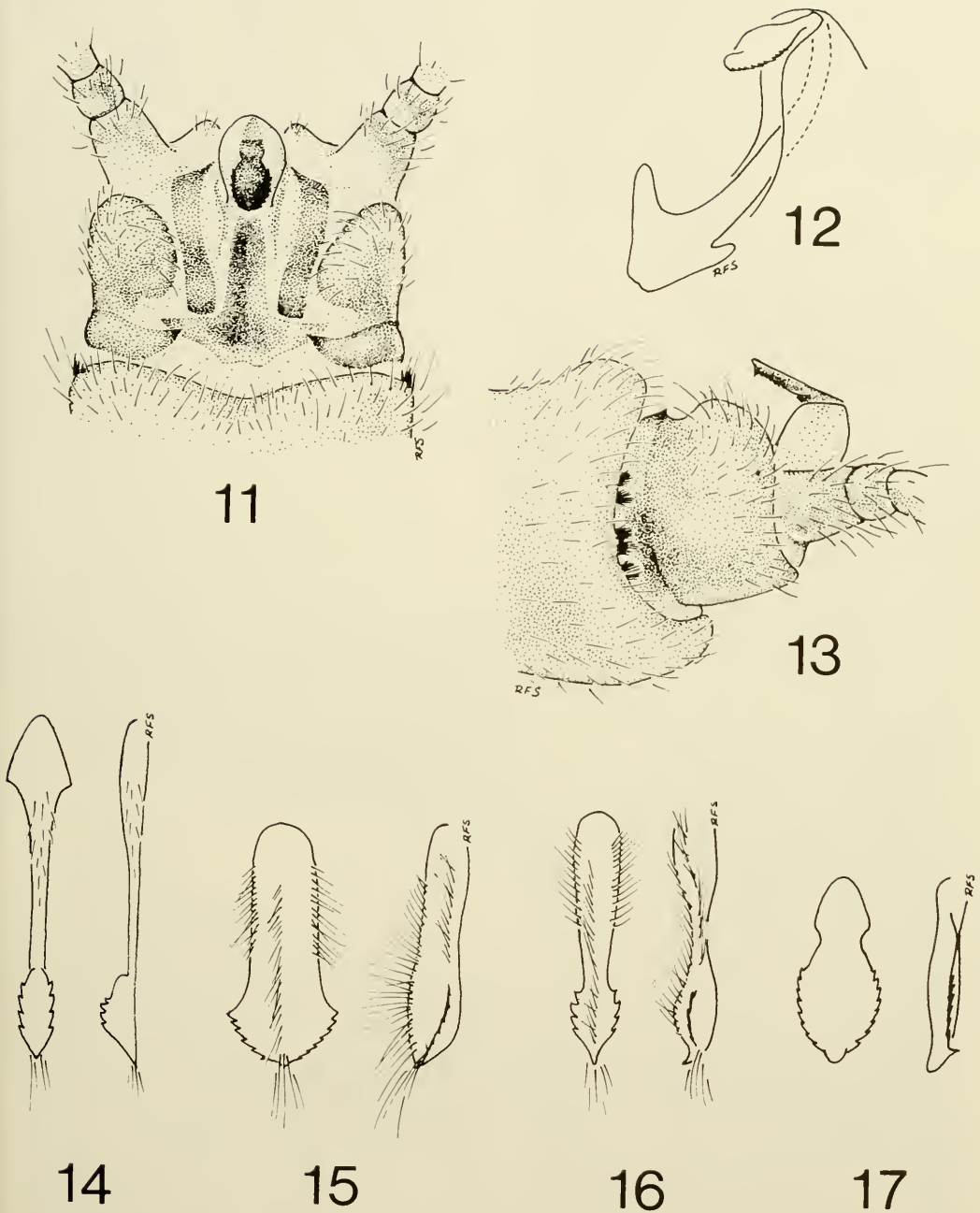
Figs. 11–13, 17

Alloperla banksi Frison, 1942: 343 (in part)

Examination of holotype, allotype, and paratypes of *Alloperla banksi* Frison revealed two specimens of a new species. Originally designated paratypes of *A. banksi*, these two specimens were of particular interest to Frison (1942) because they represented the only record of the species in Illinois. Frison's concern over the loss of habitat eliminating *A. banksi* from Illinois is even more sententious, since a separate endemic species is involved.

General color dusky in alcohol. Antennae pale basally, darker apical three-fourths; head unpatterned except for three dark ocellar rings; occiput short, lateral edges tapering posterior to compound eyes. Pronotum narrower than head, squarely oval, unpatterned, mesonotum, metanotum, and abdomen lacking dark markings. Wings macropterous, hyaline, representative of genus without reduction in venation.

MALE.—Forewing length 6.5 mm; body length 5.5 mm. Epiproct tip twice as long as wide, oval in dorsal aspect, flattened in lateral aspect, with a minute apical protrusion and serrate margins terminating before base. Cowl not enlarged. Basal anchor twice as wide as long; paragenital plates as wide as basal bar. Aedeagus membranous. Lateral brushes on segments 6 through 9.



Figs. 11-17. *Alloperla roberti*: (11) male terminalia, dorsal; (12) epiproct, $\frac{3}{4}$ view; (13) male terminalia, lateral. Epiproct tip: (14) *Alloperla imbecilla*; (15) *Alloperla banksi*; (16) *Alloperla hamata*; (17) *Alloperla roberti*.

MATERIAL.— Holotype ♂ (M.C.Z. # 32559), paratype ♂ (Illinois Natural History Survey): Illinois, Rock Island, 1860, B. D. Walsh.

ETYMOLOGY.— *Alloperla roberti* is named in honor of my father, Robert W. Surdick. An entomologist, artist, and naturalist, he has been my mentor and colleague.

DIAGNOSIS.—*Alloperla roberti* most closely resembles *A. banksi* (Fig. 15) but differs in the shape of the epiproct tip. *Alloperla roberti* bears a more ovoid, flatter epiproct tip, with longer serrated margins. *Alloperla serrata* Needham & Claassen, a western Nearctic relative, possesses a similar but more round-pillow-shaped epiproct tip with a broad anterior margin of serrations.

Triznaka spinosa, sp. nov.

Figs. 18–22

General color pale tan in alcohol. Antennae pale basally, dusky apical two-thirds; head unpatterned except for three dark ocellar rings; occiput narrow with lateral edges tapering immediately posterior to compound eyes. Pronotum rectangular, twice as wide as long, slightly narrower than head at compound eyes; corners rounded; lateral margins dusky. Mesonotum and metanotum each with dark sutures including W-mark resulting from dark recurrent scutoscutellar suture and bisecting line. Abdomen with dark median longitudinal stripe from tergum 1 tapering to 7, with lateral dusky stripes on terga 1 and 2. Cercal segments 10–11. Wings macropterous, hyaline, representative of genus.

MALE.—Forewing length 6 mm; body length 5.5 mm. Epiproct tip darkly sclerotized, thorn-shaped in all aspects, as long as wide dorsally. Basal bar nearly parallel-sided, merged with basal anchor, twice as long as greatest width, moderately sclerotized with scattered setae; paragenital plates absent. Anal lobe with scattered, posteriorly directed hairs. Tergum 9 little modified but with slight posterior curve, thickened setae. Aedeagus patterned with golden spinulae forming round patch basal to V-shaped patch with small adjacent spots and median stripe; with minute colorless scales and pair of fine terminal extensions. Hammer absent.

FEMALE.—Forewing length 7 mm; body length 7 mm. Subgenital plate with semi-circular margin in ventral aspect; basal width three-fourths width segment 8; posterior extension of flap two-thirds length segment 8; flap concave in lateral aspect. Plate evenly hirsute except for thin, hairless, slight indentation at junction of flap and posterior margin segment 8; long, evenly spaced hairs

along margin of flap, thicker towards base of flap. Segment 8 evenly fringed with long hairs on posterior margin. Sternite 9 lacking hairs medially. Vagina thickened, lightly sclerotized.

MATERIAL.—Holotype ♂, allotype, 20 ♂, 7 ♀ paratypes: California, Nevada Co., Sagehen Spring, 27-VI-1966, A. L. Sheldon (USNM #76888). Other paratypes: 2 ♀ California, Sierra Co., Salmon Crk., 11-VII-1971, D. G. Denning (USNM); 1 ♂, 1 ♀ California, Nevada Co., Sagehen Spring, 27-VI-1966, A. L. Sheldon (R. F. Surdick); 5 ♂, 5 ♀ California, Nevada Co., Sagehen Crk., Upper Carpenter Spring, 21-VII-1966, A. L. Sheldon (USNM, R. F. Surdick); 1 ♂ California, Nevada Co., Sagehen Crk., Lower Carpenter Spring, 21-VII-1966, A. L. Sheldon (USNM); 2 ♂ California, Nevada Co., Sagehen Crk., 27-VI-1966, A. L. Sheldon (USNM).

ETYMOLOGY.—The Latin adjective *spinosa* refers to the thornlike epiproct tip.

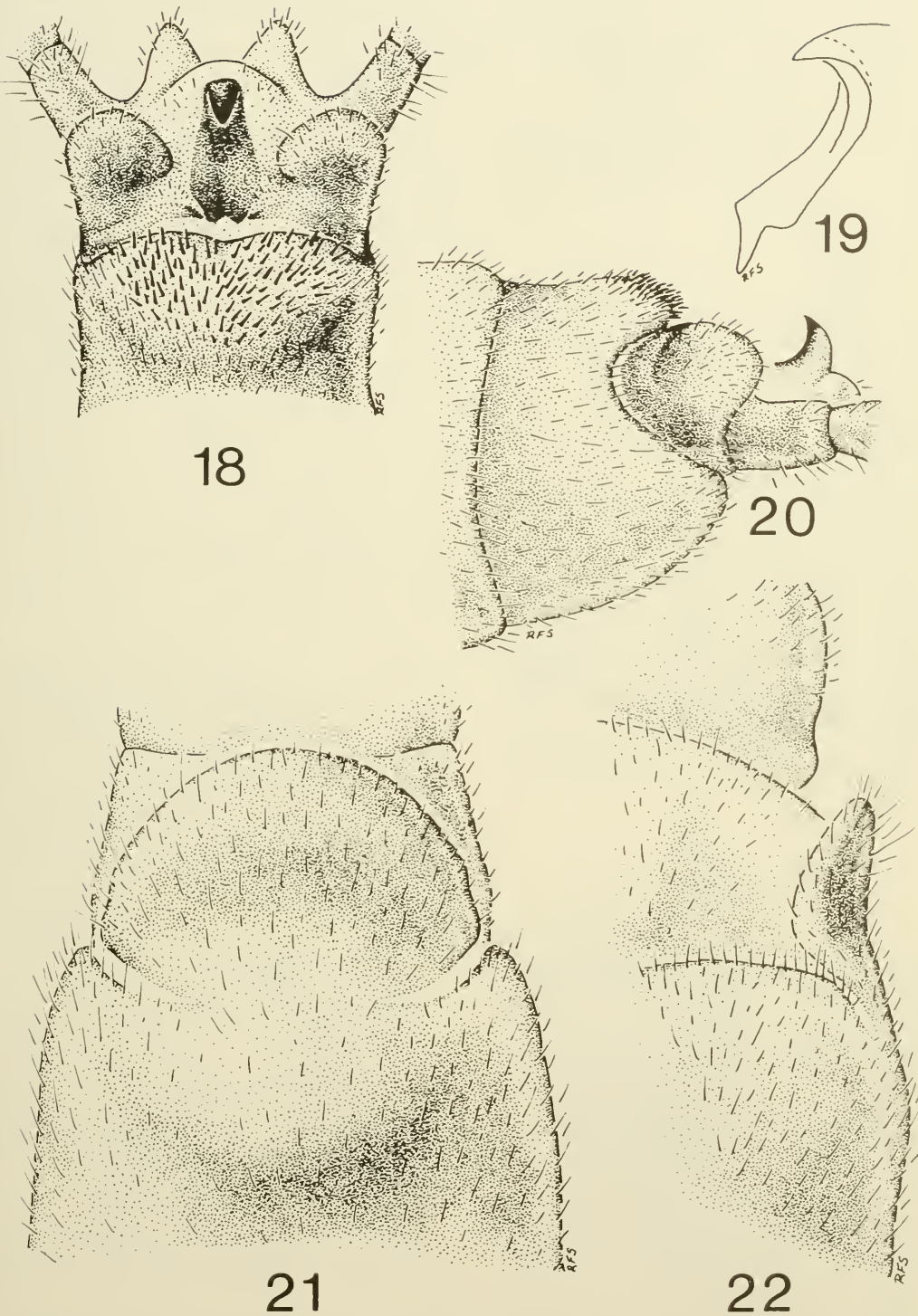
DIAGNOSIS.—*Triznaka spinosa* is distinct as the only member of the genus with an acutely pointed epiproct tip. Both *T. pintada* (Ricker) and *T. signata* (Banks) bear bluntly pointed epiprocts and are distinctly marked with black on head and thorax. *Triznaka diversa* (Frison), although similar to *T. spinosa* in pigmentation, bears a chisel-shaped epiproct tip in the male and a smaller subgenital plate flap in the female.

Bisancora, gen. nov.

Type-species: *Bisancora rutiformis*, sp. nov.

General body form and head shape representative of Chloroperlinae. Pronotum square with rounded corners; margin of equal width. Mesobasisternal Y-ridge with median ridge extending nearly to mesosternacosta. Wing venation representative of Chloroperlinae, lacking reductions, macropterous, hyaline.

MALE.—Terminal abdominal segments with lateral brushes; hammer absent; segments 7–9 unmodified except for slight medial indentation of posterior margin of tergum 9; tergum 10 completely cleft. Epiproct erectile; tip hinged, recurved, variously flattened and curved or curled; basal rod and paragenital plates equally wide, sclerotized; basal anchor double with width of large anterior anchor half of segment width, width of



Figs. 18-22. *Triznaka spinosa*: (18) male terminalia, dorsal; (19) epiproct, $\frac{3}{4}$ view; (20) male terminalia, lateral; (21) female terminalia, ventral; (22) female terminalia, lateral.

sequential posterior anchor one-fourth segment width. Aedeagus terminating in four large processes; dorsal flaps variously lightly sclerotized; ventral digitate extensions and remainder of aedeagus membranous.

FEMALE.—Terminal abdominal segments with lateral brushes, lacking hammer. Subgenital plate distinct from remainder of sternum 8 by indentation and darker sclerotization; margin variously excised or scalloped and setose.

ETYMOLOGY.—The generic term *Bisancora* is a combination of two Latin words: *bis*, meaning twin, and *ancora*, meaning anchor. It refers to the sequentially double basal anchor. The name is feminine.

DIAGNOSIS.—The genus *Bisancora* can be distinguished from closest relatives, *Sweltsa* Ricker and *Alloperla* Banks, by the squared pronotum, brown pigmentation, and markings. The double anchor and unique epiproct tip characterize the males, and the distinctively scalloped subgenital plate characterizes the females. Both *Sweltsa* and *Alloperla* bear a more thickened or inflated epiproct tip, and, except for *Sweltsa albertensis* (Needham & Claassen), *S. lamba* (Needham & Claassen), and *S. gaufini* Baumann, a membranous aedeagus.

Presently, only two species are included in the genus, *B. rutriformis* and *B. pastina* (Jewett), comb. nov.

Bisancora rutriformis, sp. nov.

Figs. 23–32

General color light brown in alcohol. Antennae pale except for dark basal segment; head with three dark ocellar rings, medial dark rectangle anterior to occipital suture and extending to clypeus; occiput short with lateral edges tapering immediately posterior to compound eyes; mandibles with four sclerotized teeth. Pronotum narrower than head by width of compound eyes, square with rounded corners and wide, even margins; darkly pigmented along anterior and posterior margins with two longitudinal stripes bordering a median thin light stripe. Mesonotum, metanotum, and sternum dusky, with only slight darkening of recurrent scutocutellar sutures; mesobasisternal Y-ridge with median ridge extending nearly to meso-

sternacosta. Abdomen with median and lateral longitudinal dark stripes extending from tergum 1 through 8; cercal segments 7–9. Wings hyaline with dusky veins, macropterous.

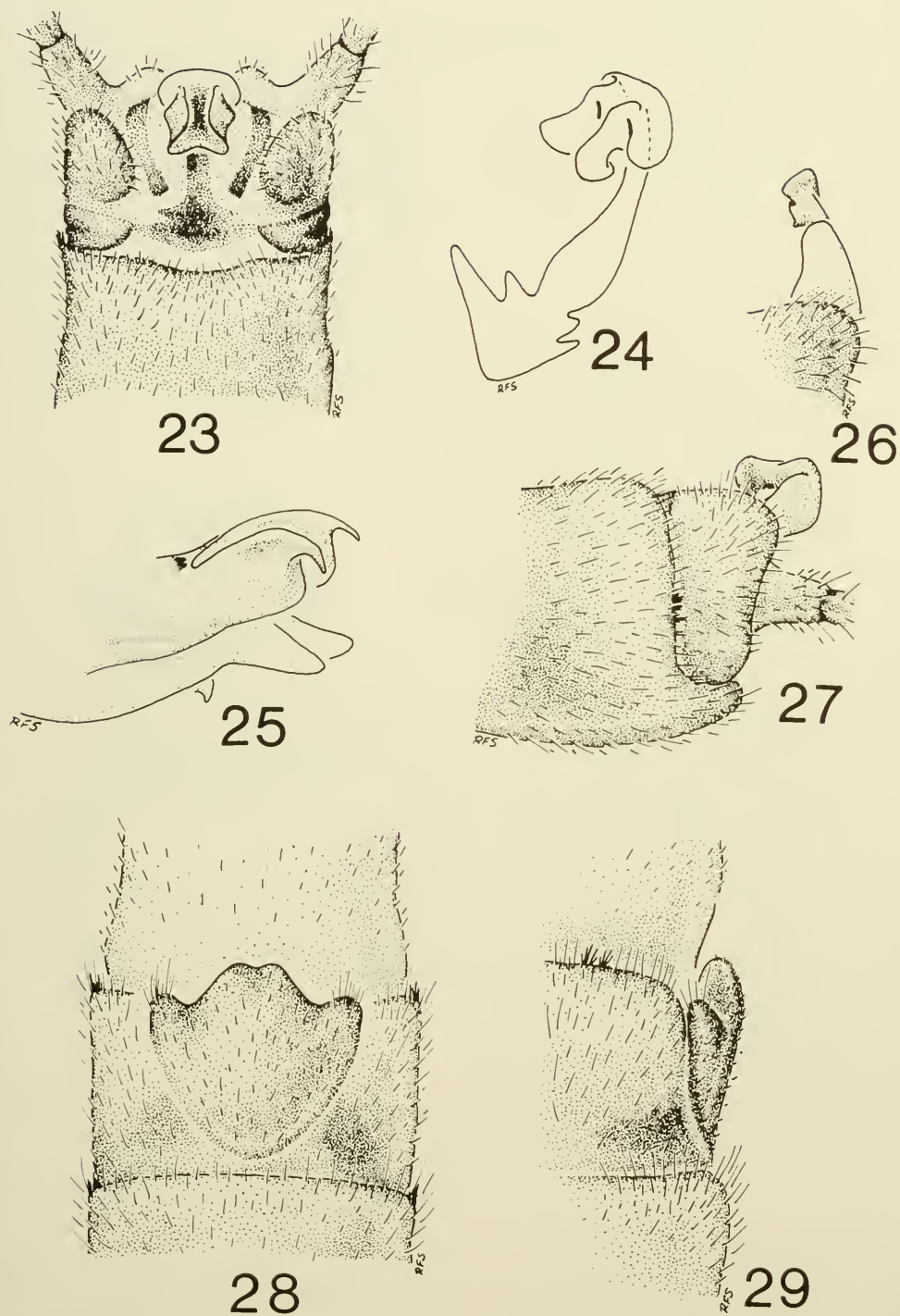
MALE.—Forewing length 5 mm; body length 4.5 mm. Epiproct tip as long as wide, moderately sclerotized, with lateral margins of thin leaflet curled dorsally forming a deep scoop; in dorsal aspect, narrow base of scoop doubles in width then narrows again distally, terminating in a flared anterior margin; in lateral aspect, greatest depth equals length, lip of scoop curled ventrally. Paragenital plates equal basal bar in width, terminate anteriorly adjacent to arms of small anchor. Large basal anchor half width of tergum 10, twice width of posteriorly successive small anchor. Tergite 9 slightly concave on posterior margin, lacking other modification of sclerite or setae. Hammer absent. Aedeagus terminating in dorsal pair of lightly sclerotized, blunt flaps and ventral pair of membranous fingers. Lateral brushes barely visible on segments 7 and 8.

FEMALE.—Forewing length 5.5 mm; body length 5.5 mm. Subgenital plate tulip-shaped, as long as wide, slightly swollen and generally more darkly pigmented than remainder of sternum, with circumference distinct by indentation and lack of setation; posterior margin forms three convex scallops, with median scallop half plate width, one-fourth plate length, and lateral scallops half size of median scallop; setation light, even except for long, dense hairs on lateral scallops. Vagina thickened, not sclerotized. Lateral brushes barely visible on segments 7 and 8.

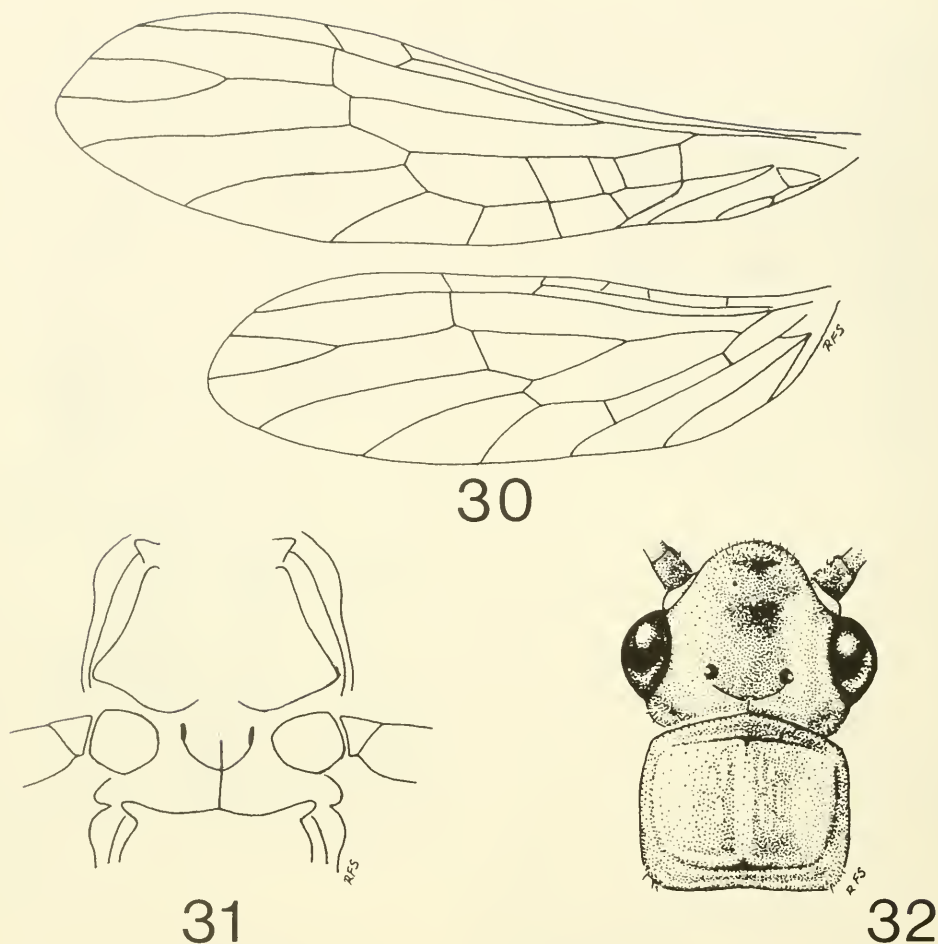
MATERIAL.—Holotype ♂, allotype (USNM #76889), paratypes 2♂, 5♀ (R. W. Baumann): California, Los Angeles Co., San Gabriel Mts., Little Rock Crk., near Little Rock and Palmdale, 9-VI-1974, C. M. Murvosh. Other paratypes: 1♂, 2♀ California, Alameda Co., Sunol Regional Park, 24-IV-1971, D. G. Denning (R. F. Surdick).

ETYMOLOGY.—The epithet *rutriformis* is a combination of the Latin words *rutrum*, meaning shovel, and *formis*, meaning shaped. It describes the flour-scoop shape of the epiproct tip.

DIAGNOSIS.—*Bisancora rutriformis* differs from *B. pastina* (Jewett) in the scooplake



Figs. 23-29. *Bisancora rutriformis*: (23) male terminalia, dorsal; (24) epiproct, 3/4 view; (25) aedeagus, 3/4 lateral view; (26) male terminalia, lateral with epiproct tip elevated; (27) male terminalia, lateral, with epiproct tip not elevated; (28) female terminalia, ventral; (29) female terminalia, lateral.



Figs. 30-32. *Bisancora rutriformis*: (30) wings; (31) mesobasisternal Y-ridge, adult; (32) adult head, pronotum.

epiproct tip and in sclerotization of the dorsal leaves of the aedeagus. *Bisancora pastina* (Figs. 33-35) bears a flat, sheetlike epiproct tip that widens distally to two thick lateral prongs. Females differ in the length of the subgenital plate produced beyond the margin of sternum 8. In *B. pastina* (Figs. 36, 37), the median scallop is half as long as in *B. rutriformis*.

Bisancora pastina (Jewett), comb. nov.
Figs. 33-37

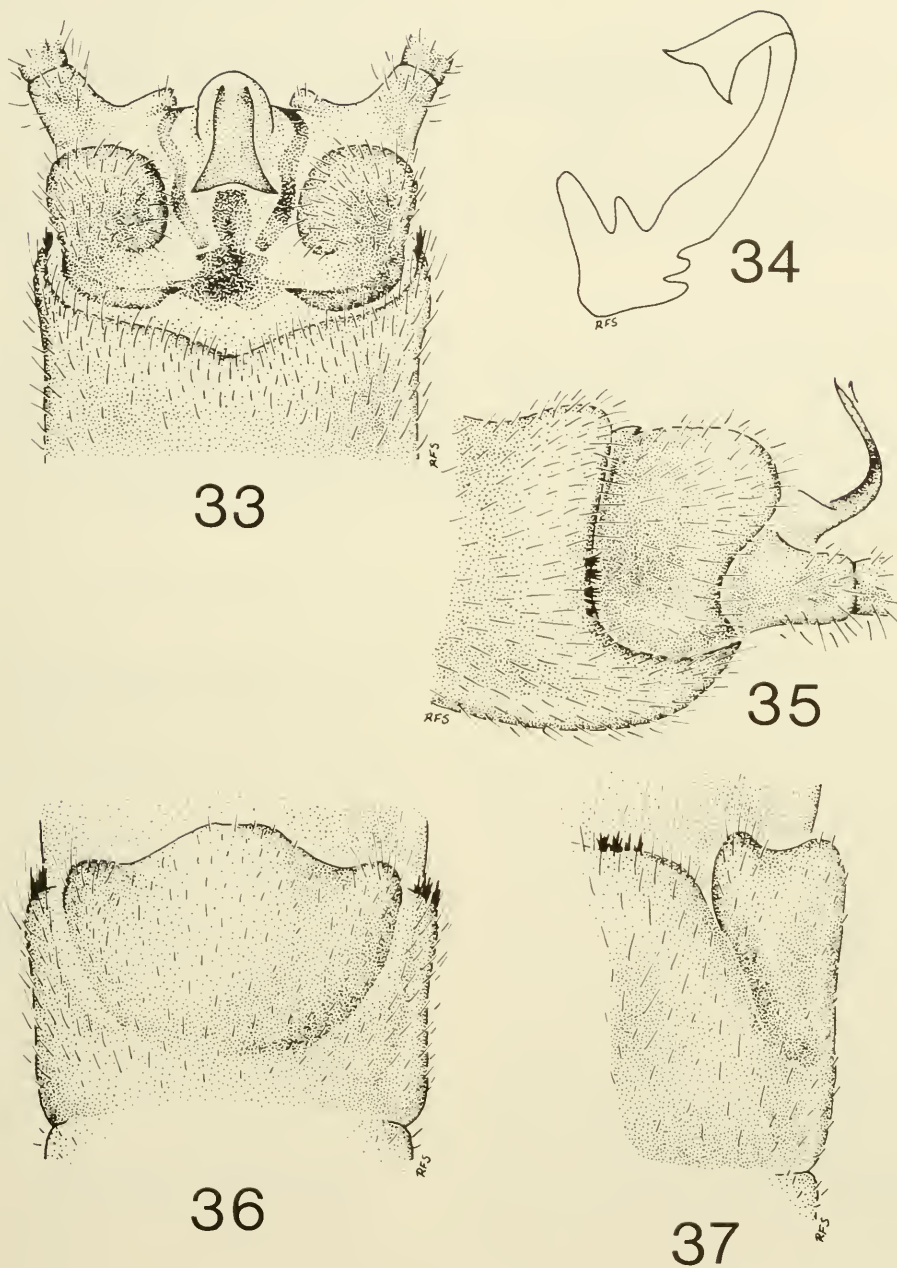
Alloperla (Sweltsa) *pastina* Jewett, 1962: 20, Fig. 6.
Sweltsa pastina: Illies, 1966: 455.

The flat epiproct tip, double basal anchor, and unmodified terminal terga, as well as similar subgenital plate, and aedeagus

indicate the affinity of *B. pastina* with *B. rutriformis*.

ACKNOWLEDGMENTS

Appreciation is extended to Dr. B. P. Stark, Mississippi College; Dr. R. W. Baumann, Brigham Young University; Dr. O. S. Flint, U.S. National Museum; Dr. J. D. Unzicker, Illinois State Natural History Survey; M. M. Peace, Museum of Comparative Zoology; Drs. E. F. Cook and P. J. Clausen, University of Minnesota; and A. M. James, Texas Instruments Corp., Dallas, for their kind assistance and loans of specimens. I am grateful for the support of the Department of Biology, University of Utah.



Figs. 33-37. *Bisancora pastina*: (33) male terminalia, dorsal; (34) epiproct, $\frac{3}{4}$ view; (35) male terminalia, lateral; (36) female terminalia, ventral; (37) female terminalia, lateral.

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ADDITIONAL BLACK-FOOTED FERRET (*MUSTELA NIGRIPES*) REPORTS FROM WYOMING

Tim W. Clark¹ and Thomas M. Campbell III²

ABSTRACT.—Thirty-nine previously unpublished reports of the endangered black-footed ferret from Wyoming are listed with dates, locations, number of animals, sources, and comments.

Historic geographic range of the black-footed ferret (*Mustela nigripes*) coincided closely with that of the prairie dog (*Cynomys* spp.), occurring over most of the Great Plains as well as semiarid grasslands and certain intermountain basins of North America (Hall and Kelson 1959, Hillman and Clark 1980). The present range is unknown, but is undoubtedly smaller than historic range due to habitat destruction and possibly other factors. Recent ferret observations and evidence, although mostly undocumented, come from South Dakota, Colorado, Wyoming, Montana, North Dakota, and Kansas.

Clark (1978, 1980) reported the historical range of ferrets in Wyoming to be nearly statewide. Ferret sightings and evidence come from nearly every county in Wyoming except Teton County and Yellowstone National Park—the same areas where prairie dogs reside. Further evidence reported by Clark (1978) showed that ferrets ranged further west in Wyoming than previously known.

Methods used by us to evaluate black-footed ferret sightings have been described (Clark 1980). This paper reports 39 previously unpublished (except Murie 1954) black-footed ferret reports from Wyoming.

ADDENDUM: A male ferret from Park County was killed by a ranch dog on 26 Sep-

tember 1981. This specimen, verified by the U.S. National Museum and the U.S. Fish and Wildlife Service, is the first complete carcass since 1965 (Clark 1980). The ferret was reported to us by Jim Lawrence of Wyoming Game and Fish Department.

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TABLE 1. Black-footed ferret reports from Wyoming in addition to those reported in Clark (1980).

Report	Date and location	Animals	Source and comments
1	ca 1875-1900, Crow Indian Nation	1	D. T. Vernon; skin in Colter Bay Indian Museum, Grant Teton National Park, Wyoming.
2	ca 1920, eastern Wyoming	10	U.S. Biological Survey (1928); killed in predator trapping programs.
3	ca 1920-30, north fork of Little Missouri River, Crook County, T57N R65,66,67W	3	W. C. Dexter, Wyoming Game & Fish Dept.; observed on prairie dog town.
4	1922, Wyoming or Nebraska	1	U.S. Biological Survey (1928); killed by trapper in Wyoming-Nebraska district.
5	ca 1940, eastern Wyoming	"a few"	W. Garst has "a few" captive black-footed ferrets (Murie 1954).
6	ca 1946-50, U.S. Hwy. 30 between Wamsutter and Rock Springs, Sweetwater County	1	P. Muchmore, Wyoming Game & Fish Dept.; road killed, skin formerly in Wyoming Game & Fish Dept. collection.
7	1948, Aug, 24 km west of Laramie on the old Jack Markely Ranch, Albany County	2	E. Cornelius, U.S. Fish & Wildlife Service trapper; trapped them in coyote sets on a prairie dog town.
8	1950s, 16 km east of Medicine Bow, Carbon County	1	J. Sterret, U.S. Fish & Wildlife Service trapper; trapped in coyote set on prairie dog town.
9	1952-53, summer, Junction County Road 610 (Marshall) and U.S. Hwy. 30, Albany County	1	A. L. Tanner, Wyoming Game & Fish Dept.; night sighting on road.
10	ca 1965, 8 km west of Rock River and north of Bailey on Cronberg Ranch, Carbon County	2	F. Long, rancher; close range daytime observation
11	1975-78, near Pathfinder National Wildlife Refuge, Carbon County	6	J. C. Marshall, ranch predator controller; observed while shooting prairie dogs.
12	1978, July, near Cottonwood Road along U.S. Hwy. 189 between Daniel and Big Piney, Sublette County	1	C. Ball, rancher; observed in Uinta ground squirrel (<i>Spermophilus armatus</i>) colony.
13	1978, near Medicine Bow, Carbon County, T22N R77W S31	1	T. M. Campbell, Biota Research & Consulting, Inc.; skull found on prairie dog town.
14	1978-79, between Kemmerer and Evanston, Uinta County; and between Hanna and Medicine Bow, Carbon County	6	S. J. Martin and M. H. Schroeder, U.S. Fish & Wildlife Service; skulls found on prairie dog towns (Martin and Schroeder 1979, 1980).
15	1979, 8 km south of Boulder along U.S. Hwy. 187, Sublette County	1	B. Kiesling, Nature Conservancy; observed with ground squirrel in mouth.

POCKET GOPHERS (*THOMOMYS TALPOIDES*) IN SUCCESSIONAL STAGES OF SPRUCE-FIR FOREST IN IDAHO

Jerry H. Scrivner^{1,2} and H. Duane Smith¹

ABSTRACT.— This study examined (1) the relative abundance of the pocket gopher (*Thomomys talpoides*) in four successive stages (1–10, 11–39, 40–79, and 80+ years following disturbance) of spruce-fir forest; (2) the relationship between number of gopher sign (mounds and earth plugs) with gopher density; and (3) a method of sampling pocket gopher populations using a 500 by 4 m strip transect. The number of gopher mounds was significantly correlated with the number of earth plugs. Data were pooled and a categorical log linear analysis used to test for significant differences in pocket gopher sign between the four successive stages. The 1–10 and the 80+ -year-old sites had significantly more gopher sign than the 11–39 and the 40–79-year-old sites. No significant differences were found between the 11–39 and the 40–79-year-old sites, or between the 1–10 and the 80+ -year-old sites. The difference in population densities may be due to understory vegetation differences between the successional stages. There was a significant correlation between amount of gopher sign and gophers caught in each of the study sites. This indicates that counts of pocket gopher sign may be used to estimate pocket gopher density. The strip transect is recommended as the most appropriate method when sampling heterogeneous habitats or when there is cause to suspect gopher populations may be aggregated within the area rather than spaced randomly or regularly.

The economic importance of the pocket gopher (*Geomys*) is rarely disputed. Some regard them as beneficial in water conservation, aeration, deepening and fertilization of mountain soils (Grinnell 1923, Grinnell and Storer 1924, Taylor 1935, Storer 1947, Ellison and Aldous 1952). Others condemn them for damaging cultivated orchards (Wight 1930), inhibiting reforestation practices (Moore 1943, Tevis 1956, Crouch 1971), and increasing soil erosion (Day 1931, Gabrielson 1938, Peck 1941).

Most literature on pocket gophers refers to studies in nonforest vegetation communities. Few have studied gophers in seral stages of forest succession, and the conclusions of those who have are generally speculative or inconclusive (Davis et al. 1938, Ellison 1946, Ingles 1949). Ellison (1946) reported that most *Thomomys talpoides* activity is restricted to herbaceous vegetation and is essentially absent from areas of spruce-fir timber. Davis et al. (1938) found only small numbers of *Geomys breviceps* in timbered areas, with large numbers in open pastures. Ingles (1949) suggested that *Thomomys monticola* prefer meadows, but, as winter approaches, gophers living in meadows move beneath trees, where humus soils allow better

drainage and prevent soil from freezing. In contrast, research preliminary to this study indicated that population densities of *T. talpoides* during the summer in a mature spruce-fir forest were greater than densities of gophers in early, more open, successional stages.

One problem in studying pocket gophers is the lack of a rapid and reliable census method. Mound counts have been used (Mohr and Mohr 1936, Phillips 1936, Davis et al. 1938, Ellison and Aldous 1952, Julander et al. 1959, Howard 1961), but the validity of this method has been criticized (Richens 1965, Ingles 1949). Reid et al. (1966) proposed a method for approximating populations by counting new sign (mounds, mound clusters, and earth plugs) that appeared within a two-day interval. Following an intensive "trap-out" of the study plots, they determined there was a significant correlation between the number of gophers and the number of new sign appearing in the two-day interval. Reid et al. (1966) concluded that "the relationship between numbers of pocket gophers and ground surface sign should be determined for each new situation and season, vegetation type, and species of pocket gopher where inventory work is planned."

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The objectives of this study were to (1) determine the relative abundance of the pocket gopher (*Thomomys talpoides*) in four successional stages of spruce-fir forest; (2) determine if a relationship existed between the number of pocket gopher mounds and earth plugs with gopher density; and (3) discuss a method of sampling pocket gopher populations using a 500 by 4 m strip transect.

STUDY AREA

Study areas were located within the Pierce Ranger District of the Clearwater National Forest in Idaho. U.S. Forest Service records were consulted and study sites selected that represent a successional range from clear-cut to mature climax in the spruce-fir association. Two stands (referred to as group I and II) of each age class, 1–10, 11–39, 40–79, and 80+ years following disturbance were selected. Elevation of the study sites ranged from 708 to 1539 m. Although disturbance of the sites during the study was negligible, human activity in the Pierce District was considered high, particularly in the form of logging activity and, to a lesser extent, recreational activity. On the 1–10-year-old sites, Fireweed (*Epilobium angustifolium*) was the dominant forb, with Elderberry (*Sambucus sp.*) and Snowbrush (*Ceanothus velutinus*) the dominant shrubs. In the 11–39 and the 40–79-year-old sites, Heart-leaved Arnica (*Arnica cordifolia*) and Twin-flower (*Linnaea borealis*) were dominant forbs and Scouler Willow (*Salix scouleriana*) and Honeysuckle (*Lonicera utahensis*) were dominant shrubs in the 11–39-year-old sites. The dominant shrub in the 40–79-year-old sites was Huckleberry (*Vaccinium membranaceum*). Wild Ginger (*Asareum caudatum*) was the dominant forb in the 80+ year-old sites and Huckleberry (*V. membranaceum*) the dominant shrub. In all successional stages, Grand Fir (*Abies grandis*) was the dominant tree species.

METHODS

Because pocket gopher activity is generally highest in late summer to early fall (Miller 1948, Miller and Bond 1960, Reid et al. 1966), data were gathered during August 1979. Fifty quadrats, each 4 m in diameter,

spaced 10 m apart along a 500 m randomly established transect, were analyzed for pocket gopher activity in each of the eight study sites. Mounds and earth plugs were recorded as evidence of pocket gopher activity. Mounds are soil that gophers excavate while burrowing. When two mounds overlapped more than 50 percent, they were considered as one. Earth plugs, circular openings filled with loose soil and generally considered to result from gophers exploring the surface for food, were frequent (Grinnell 1923).

At each point along the transect a modified point quarter procedure (Phillips 1959) was implemented to gather data on shrub composition. The height of the tallest shrub 2 m from the point was measured within each quarter. When no shrubs were present within the 2 m interval, the tallest shrub within 4 m was measured. Shrubs were classified into one of three categories based on shrub height: Class I: Trace–114 cm, Class II: 115–190 cm, Class III: > 190 cm. A categorical log linear analysis technique (Bishop 1975, Feinberg 1977) was used to test separately for significant differences in abundance of sign of pocket gopher and shrub composition in the four successional stages of forest.

The Ocular Method (Daubenmire 1968) was used to measure percent forbs (by species). This method utilizes the concept that one can accurately estimate broad coverage classes even though the observer may not be able to estimate the precise cover parameter for any quadrat very accurately. Using a multiple comparison procedure described by Dunn (1964) and Gibbons (1976), simultaneous statements of statistical differences were made comparing all possible combination sets of total forb cover of two successional stages. In using this procedure the overall levels of significance are frequently larger than numbers ordinarily used in an inference involving a single comparison. We followed Gibbons's (1976) recommendation of setting α at 0.02 when comparing four populations.

To correlate pocket gopher numbers with sign, a procedure described by Reid et al. (1966) was modified and implemented. Whereas Reid et al. (1966) used 40,000 ft² (12,121 m²) plots, this study involved use of a rectangle plot. Approximately one week after

the initial inventory of transects was made, the transects were again traversed and all pocket gopher sign leveled within 2 m of each side of the transects. This resulted in a strip transect 500 by 4 m, or 0.2 ha. Twenty-four hours after the sign was leveled, the transects were examined for new pocket gopher sign and trapped intensively with Macabee traps. The traps were operated for three days to assure that all or most animals were trapped. Data from the eight study sites were pooled and a regression analysis performed to correlate pocket gopher numbers with sign produced by the animals.

RESULTS

For the eight study sites, the number of pocket gopher mounds was significantly correlated ($P < 0.05$) with the number of earth plugs (Fig. 1). This allowed the mound and earth plug data to be pooled for subsequent analyses of gopher populations.

Relative abundance of pocket gopher sign in each successional stage was examined (Fig. 2). With four successional stages of interest, three statistical comparisons were made: (1) the 1-10 and the 80+ with the 11-39 and the 40-79-year-old sites, (2) the 11-39 with the 40-79-year-old sites, and (3) the 1-10 with the 80+-year-old sites. The first contrast indicated the 1-10 and the 80+-year-

old sites had significantly ($P < 0.05$) more pocket gopher sign than the 11-39 and the 40-79-year-old sites. Although no significant difference was found between the 11-39 and the 40-79-year-old sites, there was a tendency for the 40-79 age class to have more sign than the 11-39. Finally, the 1-10 and the 80+-year-old sites did not differ significantly and there was little tendency for one successional stage to have more pocket gopher sign than the other.

Because the count of mounds and earth plugs for use in predicting pocket gopher densities had been criticized, we were interested in the predictive value of these counts in spruce-fir forests in Idaho. Counts of gopher sign, total number of gophers captured, and the number of gopher sign/gophers caught using the modified Reid et al. (1966) method as previously described are shown in Table 1. These data indicate an average of $2.5 (\pm 1.2)$ sign of gopher made for each gopher. The number of observed sign of gopher was significantly correlated ($P < 0.05$) with the number of pocket gophers caught (Fig. 3). Thus, for this area in Idaho, sign of pocket gophers may be used as a rapid and reliable means of estimating pocket gopher populations.

Of three shrub classes (Class I: Trace-114 cm, Class II: 115-190 cm, Class III: > 190 cm), early and late successional stages had significantly ($P < 0.05$) more Class I shrubs and fewer Class III shrubs than midsuccessional stages. Total forb cover was relatively

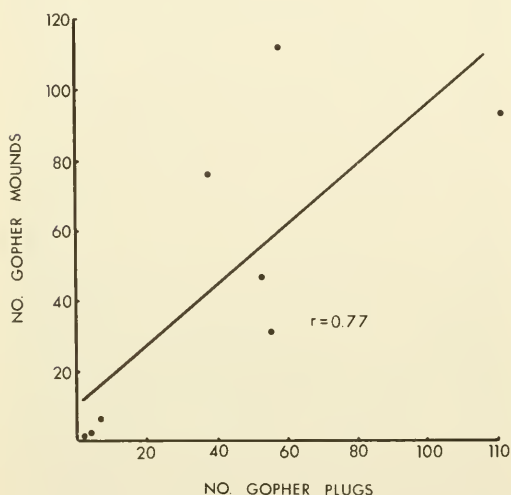


Fig. 1. Correlation of the number of pocket gopher mounds with the number of earth plugs.

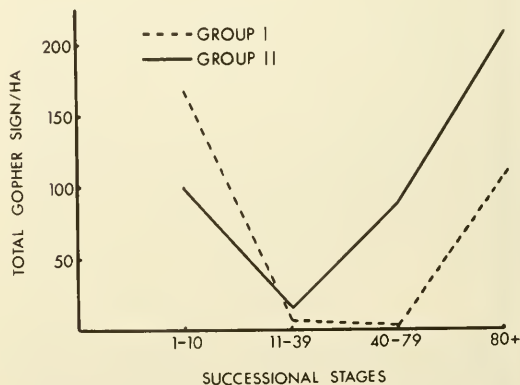


Fig. 2. Total number of pocket gopher signs (mounds and earth plugs)/ha in two groups of four successional stages.

TABLE 1. Total number of gopher sign (mounds and earth plugs), total gophers caught, and the number of gopher sign produced in two groups of four successional stages during August 1979.

Successional stage	Number gopher sign	Number gophers trapped	Number sign/gopher
1-10 ^a b	39	15	2.6
1-10 II	16	8	2.0
11-39 I	1	1	1.0
11-39 II	15	10	1.5
40-79 I	3	1	3.0
40-79 II	55	16	3.4
80+ I	24	5	4.8
80+ II	35	22	1.6
Total	188	78	2.5

^aYears following disturbance.

^bGroup designation.

constant in all successional stages (Table 2). In group I sites there were no significant differences in forb cover of the 1-10, 40-79, and 80+ -year-old sites; however, these sites contained significantly greater cover than the 11-39-year-old site. In group II sites the 80+ -year-old site contained significantly more forb cover than the 11-39-year-old site, but other sites did not differ significantly.

DISCUSSION

Several authors (Scheffer 1931, Crouch 1933, Miller 1948, Laycock 1957, Miller and Bond 1960, Howard and Childs 1959) have reported that burrowing activity of pocket gophers varies seasonally. Most agree that activity is highest in spring, tapers to a low in summer, increases in late summer to early

TABLE 2. Results of Dunn's (1964) multiple comparison test forb cover in two groups of four successional stages. Underlined successional stages do not differ significantly ($\alpha = 0.20$). Percent forb cover is also included.

Group I	11-39 ^a	80+	1-10	40-79
Total forb cover(%)	27.1	30.0	41.2	46.7
Group II	11-39	1-10	40-79	80+
Total forb cover (%)	34.1	39.6	40.8	47.6

^aYears following disturbance.

fall, then stabilizes to a moderate level through winter. Some (Crouch 1933, Miller 1948, Laycock 1957) attribute variation in observed burrowing to fluctuations in soil moisture and soil temperature. Others (Miller and Bond 1960, Reid et al. 1966) found little correlation between burrowing and soil moisture and suggest that late summer burrowing activity represents behavioral changes associated with dispersal of young. Reid et al. (1966) noted that because of this seasonal difference in rate of sign made by pocket gophers, results of sign counts in summer would differ from those in fall. Pocket gopher densities based on midsummer sign counts would be underestimated and more accurate estimates would be expected as fall approaches. Data were gathered in August, and there was a good correlation between estimates of pocket gopher density and sign counted.

Much of the literature dealing with pocket gophers in forest ecosystems refers primarily to the abundance and role of gophers with respect to early stages of reforestation (Dingle 1956, Garrison and Moore 1956, Tevis 1956, Crouch 1971, Hooven 1971). It is not surprising, therefore, to find pocket gophers in particularly high numbers in early successional stages, but the high density of pocket gophers in the mature forest was neither really known nor expected. While a definitive explanation of this distribution is not intuitively obvious, some suggestions may be offered.

Gopher distribution could be influenced by vegetation differences between seral stages. Early and late stages had more small shrubs and fewer tall shrubs than midsuccessional stages due to the increased woody root system of large shrubs. *Thomomys talpoides* prefer deep, rich, tractable soils (Miller 1964).

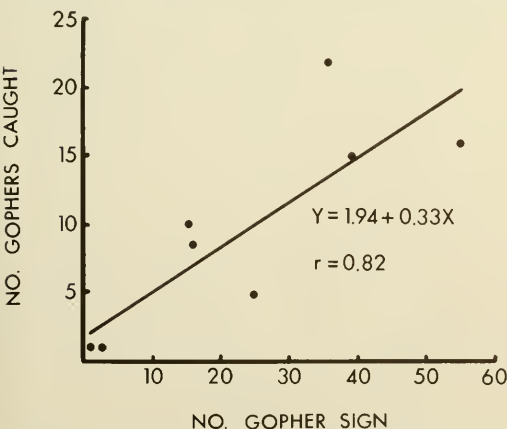


Fig. 3. Number of observed sign of pocket gopher correlated with number of pocket gophers caught in two groups of four successional stages.

Though the soil in these midsuccessional stages may be deep and rich, gophers may find the root-laden soil unfavorable for burrowing.

In addition, pocket gophers prefer herbaceous vegetation for food. Although there were few significant differences in total forb cover among the successional stages, the sites differed in species composition. *Thomomys talpoides* could prefer forbs in early and late successional stages. Motyka et al. (1950) similarity index indicated that the 11–39 and the 40–79-year-old sites were most alike, i.e., had the greatest similarity index, in both groups of successional stages. The smaller population densities of gophers in midsuccessional stages could be attributed to less palatable forbs these sites have in common.

Although the relative distribution of shrubs and herbs within the four successional stages may be the most apparent explanation of pocket gopher distribution, other less obvious habitat differences may be equally important. Such soil characteristics as temperature, moisture, pH, texture, and profile may differ between successional stages and influence gopher distribution.

The final objective of this study was to discuss the strip transect method of sampling pocket gopher populations. Theoretically, plot size can influence the variance of the sample mean (and thus cost required to achieve an adequate sample size), relative border decisions, ease of establishing a permanently marked plot, and movement required to observe plot contents (Curtis and McIntosh 1950, Cottam et al. 1955, 1957). The first effect of plot shape (i.e., influence on variance of the sample mean) would not be expected to be a problem in a relatively homogeneous habitat where pocket gopher populations may be randomly or regularly distributed. In a heterogeneous habitat, however, gopher populations may be aggregated into favorable microhabitats. In this case, there is a strong likelihood that isodiametric plots may fully include or not include aggregations of gopher populations. In contrast, the strip transect is more likely to sample regions of differing degrees of aggregation. Theoretically, one would thus expect the strip transect plot to have a smaller variance

than would isodiametric plots of comparable size.

Though the variance may be smaller with the strip transect, greater movement of the researcher may be necessary to determine whether to include a specific gopher sign. As the length of the transect increases, the number of border decisions increases. Such decisions take time and increase the likelihood of sampling bias.

This method of sampling pocket gopher populations requires permanently marked study plots. Although it is somewhat easier to permanently mark square or round plots, we had little difficulty marking the strip transect and judging any marking differences inconsequential.

In summary, when studying pocket gopher populations, we recommend, on a theoretical basis, the strip transect as most appropriate when sampling heterogeneous habitats or when there is cause to suspect gopher populations to be aggregated within the area of interest rather than randomly or regularly spaced.

ACKNOWLEDGMENT

This research was supported by the Canada/U.S. Spruce Budworm Program.

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UNUSUAL TOOTH WEAR IN ELK AT GLACIER NATIONAL PARK, MONTANA

Keith Shaw¹

ABSTRACT.— An unusual wear pattern in the cheek teeth of elk-wapiti, in which the third premolars and first molars of the upper jaw wear excessively into corresponding teeth in the lower jaw, was found in a Glacier National Park, Montana, elk skull. This unusual wear pattern was previously reported from elk of the Yellowstone-Jackson, Wyoming, herd.

Sometime during the winter of 1975-76 a cow elk or wapiti (*Cervus canadensis* = *C. elaphus*) died on the Two Dog Flats winter range of northeastern Glacier National Park, Montana. The carcass was cleaned up by coyotes, ravens, and other small scavengers and the bones scattered. Glacier Park Ranger Lloyd Kortge and I found the nearly intact skull and lower jaw and were immediately impressed by the seemingly unusual pattern of cheek teeth wear. Olaus Murie (1951) has diagrammed a similar wear pattern for elk of the Yellowstone-Jackson, Wyoming, herds with the note that: "...The profile of the lower row [of teeth] is concave; that of the upper row is convex. This relationship sometimes becomes greatly accentuated in old age. There is a tendency for an angle to form in the upper jaw, the projecting point being formed by the first molar, sometimes in combination with the adjacent premolar; and this angle wears a depression near the middle of the lower row. Sometimes the second molar forms the point of the protruding angle. Because of this feature, the first lower molar may be worn out and have only the roots remaining or may be missing even while in the same jaw the anterior premolar is still sound and only moderately worn. . . ."

The Two Dog Flats elk skull has complete dentition and adjacent parts of the third premolar and first molar form the triangular point, projecting 7 mm beyond the level of adjacent teeth in the right upper jaw (Fig. 1), and 7 mm beyond that level in the left upper jaw (Fig. 2). Corresponding depressions were worn to a 14 mm depth on the right side into

the first molar of the lower jaw (Fig. 1), and to a 12 mm depth in the first molar on the left-side lower jaw (Fig. 2). The increased wear depth on the right has completely separated the first molar into posterior and anterior halves. Lower jaw maximum wear down probably reached to the gum level, but with 4 mm on the lower right first molar and 3 mm on the lower left first molar still projecting above the jaw bone. The second molars in the lower jaw have each worn a corresponding deep groove into the posterior half of each of the upper jaw first molars.

There is apparent necrosis of the bone along the inside of the left third molar of the upper jaw, but no evidence of necrotic erosion in the lower jaw bone. Articulation of the mandibular joints appears normal with food grinding capability at the time of death. The paunch of the dead elk was packed with forage of apparent adequate quality. The Two Dog Flats herd has not suffered any appreciable winter mortality in recent years traceable to range depletion. The exact cause of death of this cow elk was never determined and cannot with certainty be attributed to this unusual tooth wear.

Less than 300 m from the cow elk death site a mature bull elk also died of undetermined causes during the same winter. Teeth in the upper jaw of this elk showed no similarity to the wear pattern found in the cow elk skull.

As pointed out by Murie (1951), after its fourth year the age of an elk cannot be told with precision by the teeth. It can only be assumed then that both these Two Dog Flats

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elk were mature, that is, between the ages of 5 and 10, because none of the incisors showed the wear and tooth loss found in elk more than 10 years old.

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Fig. 1. Right side view of Glacier National Park cow elk skull showing unusual cheek teeth wear.



Fig. 2. Left side view of same cow elk skull.

SEED DISPERSAL IN HYBRID *SALSOLA*

M. A. B. Lee^{1,2} and Timothy Brothers¹

ABSTRACT.— The study population is a group of hybrids of *Salsola iberica* × *S. paulsenii*. The plants show great variation in phenotypic characteristics, and the character complexes of the parent species seem to have largely disappeared. Seeds are dispersed both locally, from intact plants, and by tumbling. Tumbling is the dominant form of dispersal in most individuals studied. Most locally dispersed seeds fall between .5 and 1.5 m from the parent plant. Despite the dominance of tumbling, large numbers of seeds are dispersed locally and probably serve to maintain the population while those dispersed by tumbling introduce the plants into new areas.

Tumbling is a form of seed dispersal where the entire plant or certain parts of the plant detach and are blown along the ground by the wind, dispersing seeds with the movement. Van der Pijl (1972) mentions a number of species that disperse seeds in this manner and describes different types of modifications associated with this dispersal mode. These modifications include the upward curving of the plant to better attain a spherical shape, and methods of detachment for the tumbling parts. Becker (1978) has studied the process of detachment or abscission in *Kochia scoparia* and concludes that although the actual detachment is caused by the wind, internal desiccation of stem tissue is an important first step in this process. One of the few quantitative studies of tumbling dispersal was done on *Agrostis hiemalis* (Rabinowitz and Rapp, 1979). They showed that this grass has both stationary dispersal, when the seeds fall from the plants in place; and tumbling dispersal, during which the panicle detaches and tumbles, dispersing seeds over greater distances. Approximately half the seeds are dispersed by each mode.

One of the most commonly observed tumbling plants is *Salsola* spp., commonly known as tumbleweed or Russian thistle. This is an introduced plant in the United States, native to Eurasia. Beatley (1973) lists three species found in the U.S. and notes that the two most common, *S. paulsenii* Litv. and *S. iberica* Sennen & Pau., hybridize freely.

Salsola iberica is sometimes referred to as *S. kali* L. var. *tenufolia* Tausch.

In a study of *Salsola iberica*, Evans and Young (1972) noted that seed dispersal from plants in place is slight, and concluded that tumbling is necessary for effective seed dispersal in this species. In a similar study of *S. paulsenii*, these same authors concluded that most of the seeds of this species disperse locally before the plant tumbles (Young and Evans, 1979). In both studies, seed dispersal was evaluated by taking soil and litter samples at various distances from intact plants and germinating the seeds in these samples. Our study investigates seed dispersal in a population of hybrids of these two species.

METHODS

The population chosen for study was located in the Jones Reserve, part of the Natural Land and Water Reserve System of the University of California. This reserve is located in the Santa Monica Mountain Range, Los Angeles County, California. *Salsola* is an important part of the roadside vegetation in this area. A mile-long section of road was chosen as the study site. When the study began in October 1980, seeds were ripening on the *Salsola* in the site but little if any dispersal had occurred.

The population was sampled to determine the species of *Salsola* present. Every fifth individual along both sides of the road was

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sampled. These were taken to the laboratory and described. Beatley (1973) lists the distinguishing characteristics of *Salsola iberica* and *S. paulsenii*. We chose five of these on which to base our analysis of the study population (Table 1). Calyx size and leaf length were determined by measuring to the nearest millimeter the largest calyx and longest leaf present. Foliage color was judged by comparison of individual samples. Calyx color and stem striations were noted. Other differences between the two species mentioned by Beatley (1973) were not used because they apply only to immature plants.

The study population showed a great deal of variation in the size of individuals. To reduce this, only individuals between 1 and 1.4 meters in height were selected for the remaining parts of the research. Most of the mature individuals in the study site fell within this height range.

Eight plants were selected for local seed dispersal studies. Seed traps were constructed of petri dishes 9 cm in diameter, in which were placed filter paper covered with Tangletrap (Werner 1975). These traps were placed around the selected plants in four cardinal compass directions at the base of the plant and then at .5 m intervals to a distance of 1.5 m. Seed traps were anchored at ground level. Tall vegetation surrounding these plants and all *Salsola* within 4 m of the plant were removed. The traps were checked weekly and filter papers changed as necessary. Trapping continued until the plants broke off and tumbled, which occurred between late November and early January.

To estimate the proportion of seeds dispersed locally we chose an additional 10 individuals in the field. These plants were monitored and sampled when they were ready to

tumble. Plants were judged to be ready to tumble by pulling gently at the base. If the stem broke, the plant was sampled; if not the individual was left until a later date. For each plant, two branches were randomly chosen. The number of seeds remaining on the branch and the number of empty seed bracts were counted. These data were used to compute the proportion of seeds dispersed locally before tumbling.

RESULTS

Study Population

There was a great deal of variation in the study population in most of the phenotypic characteristics chosen for study (Table 2). The majority of the sampled plants (42 plants, 60 percent of the sample) had both pale and red stem striations, or pale striations with splotches of red at the branch nodes. These were categorized as intermediate between *Salsola iberica* and *S. paulsenii*. Only 36 percent of the sample (25 plants) had pale striations, characteristic of *S. paulsenii*, and 4 percent (3 plants) had all red purple striations, characteristic of *S. iberica*.

Calyx color in all sampled individuals was pale or pale with some red near the base of the calyx wings, and all were categorized as *S. paulsenii* in this characteristic. Foliage color was more variable. Forty-four percent (31 plants) had blue green foliage and were categorized as *S. iberica*, 29 percent of the sample (20 plants) were judged to have yellow green foliage (*S. paulsenii*), and 27 percent (19 plants) were intermediate.

Calyx size varied between 2.5 and 4 mm but on most plants fell between 3 and 3.5 mm. The calyx of *S. iberica* is usually less

TABLE 1. Distinguishing characteristics, *Salsola paulsenii* v. *S. iberica*^a.

Character	<i>S. paulsenii</i>	<i>S. iberica</i>
Plant color	Yellow green	Blue green
Stem striations	Pale or none	Red purple
Calyx color	Colorless or pale pink, usually red near base of wings	Deep red
Calyx size	3-4 mm	2 mm
Leaf length	.5-1.5 cm	2 cm

^aAfter Beatley, 1973.

TABLE 2. Characteristics of the study population.

Character	Percentage of sampled individuals ^a		
	<i>S. paulsenii</i>	Intermediate	<i>S. iberica</i>
Stem striations	36	60	4
Calyx color	100	0	0
Foliage color	29	27	44
Calyx size	63	37	0
Leaf length	61	0	39

^aTotal number of plants sampled = 70.

than 2 mm (Beatley 1973), so all the individuals sampled appeared to be either intermediate between the two species, or *S. paulsenii*, which has calyx wings of 3 to 4 mm.

Leaf length showed a pattern of variation similar to calyx size. Leaves varied between .6 and 3.7 cm, but the majority of the sample fell between 1 and 2.3 cm. Thirty-nine percent of the sample had leaves of 1.5 cm or less and were classified as *S. iberica*; the remainder were categorized as *S. paulsenii*.

These characteristics do not seem closely linked in individuals (Fig. 1). Individuals with yellow green foliage seem somewhat more likely to have calyxes of 3.5 mm and leaves of about 1 cm (all *S. paulsenii* characteristics) and those with blue green foliage tend to have *S. iberica* characteristics in leaf length and calyx size. But this is an extremely weak trend and is largely overshadowed by the great variation in most of the characteristics. These results seem to indicate that the population is made up of hybrids of these two species. It is probably an old, established hybrid population in which the character complexes

of the original species have largely disappeared.

Pattern of Local Seed Dispersal

Seed traps placed around eight individuals were used to determine the pattern of local seed dispersal. The average number of seeds trapped at each distance for each plant is shown in Figure 2. Two types of patterns can be seen in these graphs. Most of the individuals (Nos. 2, 3, 6, 7, 8) show a general decrease in density of seed dispersal with increasing distance from the plant. In one of these individuals (Plant No. 8), traps at .5 m caught more seeds than those at the base of the plant, but the density of seed fall then decreased with distance. Although the size of the plants varied somewhat, traps at .5 m were in all cases under the canopy of the plant, usually quite close to the edge of the canopy, and those at 1 m were outside the canopy. These individuals then show more dense seed dispersal under the canopy with decreasing seed density at increasing

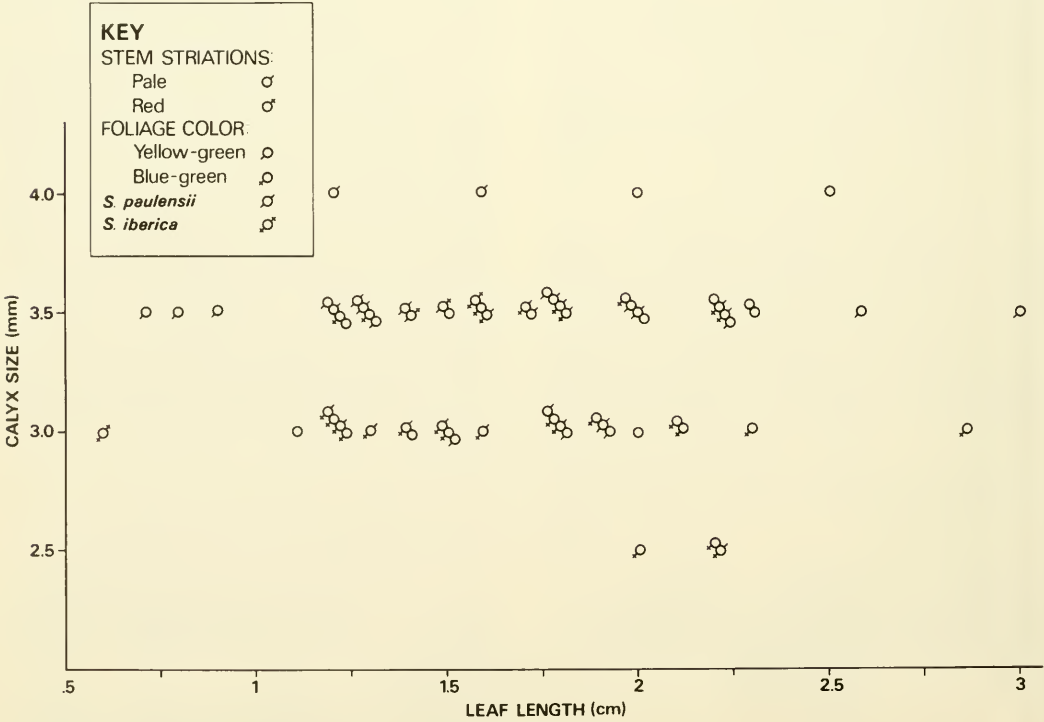


Fig. 1. Scatter diagram showing characteristics of study population. Each dot represents one sampled plant. Stem striations and foliage color shown as oblique lines and crosses. Lack of these symbols indicates intermediate characteristics as explained in the text.

distance. Plants 4 and 5 have a somewhat different pattern. Here seeds are more densely dispersed at 1 m than under the canopy. In both these generalized patterns, few seeds were caught at 1.5 m. Plant No. 1 is anomalous in that seed density increases with increasing distance.

These data describe only the density of seed fall at a given distance from the plant, not the actual number of seeds that fall at that distance. The total number of seeds that disperse within a given distance can be computed only by taking into consideration the size of the area. In a circular formation such as that represented by these seed traps, the area in each distance interval varies greatly. For example, the circle around the plant formed by the traps placed at the base of the plant has an area of .0254 m². The most distant traps, placed at 1.5 m from the plant, sample a ring-shaped area, .5 m in width, with a total area of 3.972 m². Additionally, these traps sample seed fall density only at

the edges of these rings, and the density obviously changes over the interval. To compute the number of seeds that fall at each distance, a dispersal curve was drawn for each distance interval, using the average number of seeds caught at each distance as the end points. This curve was then rotated 360 degrees around the origin (base of the plant) to produce a solid. The volume of this solid was computed to estimate the total number of seeds that fell into the area. For this analysis, it was assumed that seeds were not dispersed beyond 2 m from the parent plant, and the dispersal curve was extended to 0 seeds at a distance of 2 m.

When this procedure is followed, the local dispersal patterns are changed somewhat (Fig. 3). In all cases more seeds fell between .5 and 1 m than fell directly under the plant (between the base and .5 m). Between 1 and 1.5 m seed fall varies. For some individuals it is greater than at closer distances; in others it is smaller. Between 1.5 and 2 m total seed

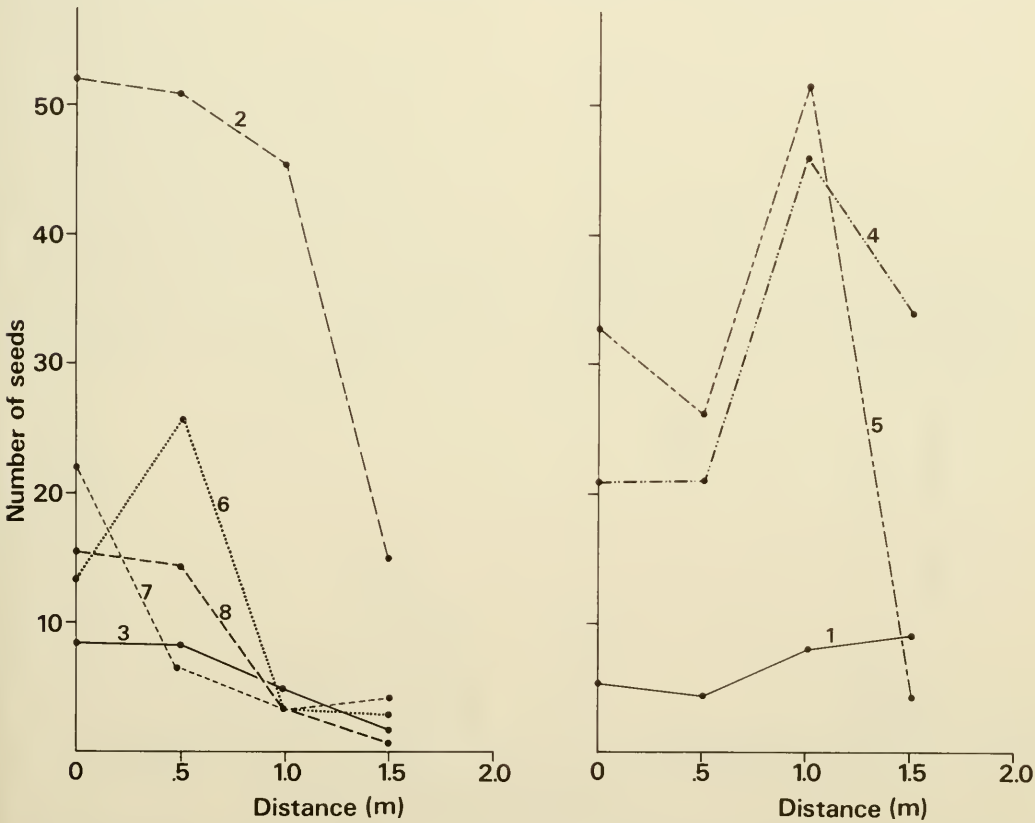


Fig. 2. Average number of seeds caught in traps placed around eight plants. Each plant is shown separately. Four traps were placed at each distance, as described in the text.

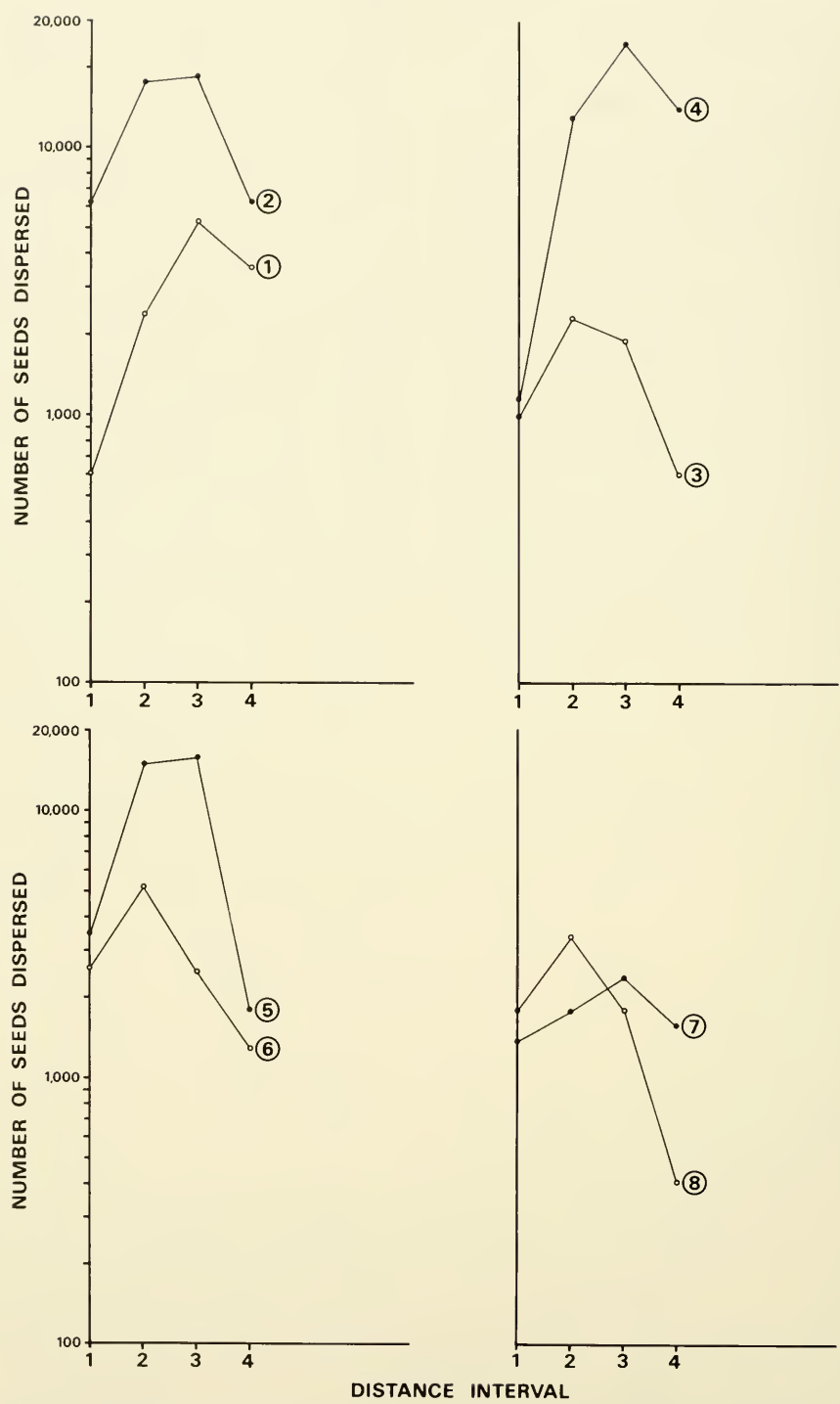


Fig. 3. Total number of seeds (on a logarithmic scale) dispersed in each distance interval. Each plant is shown separately. The method for determining total seed fall based on samples from seed traps is explained in the text.

fall also varies, but it is always less than the previous interval. In several cases (e.g., Nos. 1, 4, 5), however, seed fall in the most distant area is actually greater than directly under the plant.

The proportion of locally dispersed seeds in each distance interval is shown in Table 3. In all cases 60 percent or more of the seeds fall between .5 and 1.5 m from the plant. The proportions falling closer to the plant, at distances up to .5 m, and further away (between 1.5 and 2 m) show more variation among the individuals sampled.

The heavy seed fall between .5 and 1.5 m is probably in part a result of the fact that more seeds are borne toward the branch tips than near the stem. There is obviously some lateral movement of seeds, probably enhanced by wind.

Importance of Local Dispersal

The importance of local seed dispersal was evaluated by counting the number of empty seed bracts and the number of seeds remaining on two branches of each of 10 individuals. The proportion of seeds falling before tumbling ranged from 12 to 64 percent, with a mean value of 29.5 percent (Fig. 4). Five of the 10 sampled plants dispersed between 20 and 30 percent of their seeds before tumbling. Only two plants dispersed less than 20 percent locally, and only one dispersed more than 50 percent of its seeds locally. Tumbling then remains an important mode of seed dispersal in this hybrid population.

Although a relatively low proportion of the seeds are dispersed in the immediate area of the parent plant, this proportion represents a large number of seeds. Total number of locally dispersed seeds, as estimated from the dispersal curves, is shown in Table 3. These estimates vary among the individuals, but even the smallest, plant No. 3, is slightly over 6,000 seeds.

CONCLUSIONS

The study population is a group of hybrid individuals of *Salsola paulsenii* × *S. iberica*. Individual plants show wide phenotypic variation. It is apparently an old population in which the original character complexes have disappeared.

Seeds from these plants are dispersed both locally, from intact plants, and by tumbling. Although there is some variation among the individuals in the importance of these two modes, most sampled plants disperse 30 percent or less of their seeds locally. Patterns of local seed dispersal indicate that the largest proportion of these seeds (60 percent or more) fall between .5 and 1.5 m from the parent plant. These results contrast with those found in *Agrostis hiemalis*, a grass that also has dual dispersal modes. In that species local dispersal and tumbling are about equally important in terms of the proportion of seeds dispersed, and locally dispersed seeds fall closer to the parent plant, about 50 percent within .46 m (Rabinowitz and Rapp 1979).

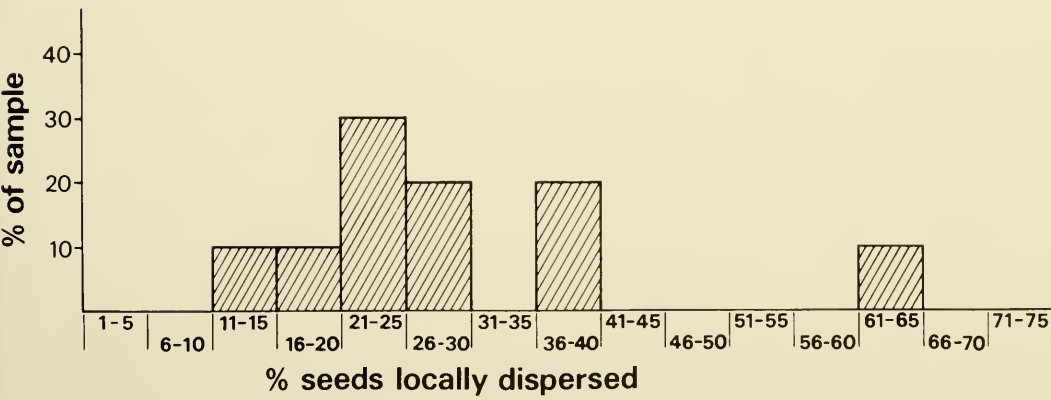


Fig. 4. Proportion of seeds dispersed locally. Data are given as average percentage of seeds dispersed before tumbling for ten sampled plants.

TABLE 3. Proportion of locally dispersed seeds in each distance interval.

Plant number	Percent of seeds in each interval				Total number of seeds dispersed locally
	0-.5m	.5-1m	1-1.5m	1.5-2m	
1	5.2	20.5	43.8	30.4	11,831
2	13.0	36.6	37.4	13.0	48,557
3	17.1	38.7	32.3	11.9	6,028
4	4.8	23.9	45.3	26.0	54,506
5	9.6	40.8	44.6	5.0	36,618
6	22.4	44.5	21.5	11.6	11,745
7	19.7	25.1	32.7	22.5	7,325
8	24.0	45.7	24.8	5.5	7,530

The dual dispersal modes exhibited by these hybrids is apparently a combination of the principal dispersal strategies used by the two parent species. *Salsola iberica* disperses seed mainly by tumbling, and *S. paulsenii* is more heavily dependent upon local dispersal (Young and Evans 1979, Evans and Young 1972). Although tumbling appears to be the dominant method in this hybrid population, the large number of seeds produced by these plants suggest that significant numbers of seeds are dispersed in the immediate area of the parent plant. These seeds probably serve to maintain the population, and those dispersed by tumbling spread the species to new areas.

ACKNOWLEDGMENTS

The authors would like to express their thanks to George Malanson, Department of Geography, University of California, Los Angeles, for his helpful advice and comments, and to Herbert Donald Enderton, School of

Engineering, University of California, Berkeley, for assistance in the computations.

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THE GREAT BASIN NATURALIST

Volume 41 No. 4

December 31, 1981

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The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 41

December 31, 1981

No. 4

ELECTROPHORESIS OF ISOENZYMES OF 16 WESTERN SHRUBS: TECHNIQUE DEVELOPMENT

R. L. Leonard¹, E. D. McArthur², D. J. Weber¹, and B. W. Wood¹

ABSTRACT.— Wildland shrubs have gained considerable attention in recent years due to increasing recognition of their values as animal feed, as wildlife habitat, and for land reclamation. Better management of the shrub resource will be possible through clearer taxonomic identification and better understanding of phylogenetic relationships. This study applied polyacrylamide gel electrophoresis and further developed this technique to address genetic relationships among 16 paired shrub species (genera: *Artemisia*, *Chrysothamnus*, *Atriplex*, *Ceratoides*, *Sarcobatus*, *Purshia*, *Covania*, and *Cercocarpus* [Compositae, Chenopodiaceae, Rosaceae]). Cluster analysis of similarity values for total protein and 14 isoenzyme systems gave patterns of species relationships expected from classical morphological grounds with two minor exceptions. Isoenzyme analyses showed promise for solving taxonomic, phylogenetic, and population genetics problems.

Wildland shrubs are receiving increasing attention as their value for land reclamation, wildlife habitat, livestock feed, and other purposes are better realized (McKell 1975). Several lines of research activity are currently underway to more effectively use shrubs as a resource to improve the nutrient quality of rangeland (Welch and McArthur 1979), to reclaim mine spoils (Thames 1977), and to maintain habitat diversity for productive rangelands (Plummer et al. 1968). As the shrubs receive more attention, their taxonomic identities and relationships need clarification so they can be better managed. Work is progressing in this taxonomic clarification effort. Examples are: saltbushes (*Atriplex*), using cytogenetics (Stutz et al. 1979); rabbitbrushes (*Chrysothamnus*), using paper chromatography (McArthur et al. 1978) and morphological characteristics (Anderson

1980); and sagebrushes (*Artemisia*) using paper chromatography (Hanks et al. 1973, West et al. 1978); morphological characteristics (Winward and Tisdale 1977, McArthur and Welch, in press); and cytogenetics (McArthur et al. 1981). This study was designed to further the taxonomic clarification effort by developing a polyacrylamide gel electrophoretic technique applicable to wildland shrubs. Sixteen plant species in three major western shrub families (Rosaceae, Chenopodiaceae, Compositae) were chosen to develop and test the technique.

Electrophoresis as a technique has been demonstrated to be of value in the analysis of isoenzymes of many plant and animal species (Gottlieb 1971). Isoenzymes (isozymes) are different molecular forms of enzymes with the same catalytic activity that migrate differentially during the electrophoretic process

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(Brewer and Sing 1970). Pattern correlation of several isoenzyme systems in concert has been taken as evidence of genetic relationship (Gottlieb 1971, Crawford and Wilson 1979, Kato and Tokumasu 1979). Study of isoenzymes has been important in developmental as well as population genetic studies (Shannon 1968, Conkle 1972, Myers 1978, Hartl 1980). This study, however, is confined to technique application and development for the three shrub families. The plant relationships were evaluated by comparing the isoenzyme data with other taxonomic information.

MATERIALS AND METHODS

Plant Materials

Sixteen species of shrubs in eight pairs were chosen to develop and evaluate the technique (Table 1). The species were paired within genera according to their similar characteristics and taxonomic placement. Based

on classical taxonomy, the pairs were thought to represent various degrees of phylogenetic affinity. One-half (eight) of the species are composites, with four *Artemisia* and four *Chrysothamnus* species chosen. The remaining half were chenopod and rosaceous shrubs (four species of each). Within *Artemisia*, two species pairs (pairs one and two) were used. *Artemisia absinthium* (wormwood) and *A. frigida* (fringed sage) both belong to the subgenus *Artemisia*, whereas *A. tridentata* ssp. *tridentata* (basin big sagebrush) and *A. nova* (black sagebrush) are members of the subgenus *Tridentatae* (McArthur et al. 1979, 1981). Species pairs three and four were chosen from *Chrysothamnus*, viz. *C. parryi* ssp. *attenuatus* (Parry rabbitbrush) and *C. nauseosus* ssp. *albicaulis* (white rubber rabbitbrush) from the section (subgenus) *Nauseosi*; and *C. viscidiflorus* ssp. *lanceolatus* (mountain low rabbitbrush) and *C. linifolius* (spreading rabbitbrush) from the section *Chrysothamnus* (Hall and Clements 1923, McArthur et al. 1978). Two pairs of cheno-

TABLE 1. Sources of plant materials used in isoenzyme study of 16 shrub species.

Family and taxa	Accession ¹ and location of seed collection
Compositae	
Pair 1	
<i>Artemisia absinthium</i> (Arab) ²	Field collection, N Provo, Utah County, Utah
<i>Artemisia frigida</i> (Arfr)	U-15, Sheep Creek, Sevier County, Utah
Pair 2	
<i>Artemisia tridentata</i> ssp. <i>tridentata</i> (Artr ⁴)	U-76, Clear Creek, Sevier County, Utah
<i>Artemisia nova</i> (Arno)	U-27, East Beaver bench, Beaver County, Utah
Pair 3	
<i>Chrysothamnus parryi</i> ssp. <i>attenuatus</i> (Chpa ^a)	U-4, Ephraim Canyon, Sanpete County, Utah
<i>Chrysothamnus nauseosus</i> ssp. <i>albicaulis</i> (Chna ^a)	North Hollow, Mayfield, Sanpete County, Utah
Pair 4	
<i>Chrysothamnus viscidiflorus</i> ssp. <i>lanceolatus</i> (Chvl ¹)	U-13, Clear Creek Canyon, Sevier County, Utah
<i>Chrysothamnus linifolius</i> (Chli)	Field collection, Helper, Carbon County, Utah
Chenopodiaceae	
Pair 5	
<i>Atriplex canescens</i> (Atca)	U-103p, Rincon Blanco, Rio Arriba County, New Mexico
<i>Atriplex lentiformis</i> (Atle)	Field collection, 16 km S of Phoenix, Maricopa County, Arizona
Pair 6	
<i>Sarcobatus vermiculatus</i> (Save)	U-6, Ephraim, Sanpete County, Utah
<i>Ceratoides lanata</i> (Cela)	U-45, Diamond Mountain, Uintah County, Utah
Rosaceae	
Pair 7	
<i>Purshia tridentata</i> (Putr)	U-28, Mt. Pleasant, Sanpete County, Utah
<i>Cowania mexicana</i> ssp. <i>stansburiana</i> (Come ⁸)	U-20, American Fork, Utah County, Utah
Pair 8	
<i>Cercocarpus montanus</i> (Cemo)	U-28, Salina Canyon, Sevier County, Utah
<i>Cercocarpus ledifolius</i> (Cele)	U-42, East of Milford, Beaver County, Utah

¹Taxa with "U" numbers assigned are plants from native accessions maintained at the Snow Field Station uniform garden in Ephraim, Utah.
²Taxa abbreviations adapted from Plummer et al. 1977.

pod shrubs were chosen. *Atriplex canescens* (fourwing saltbush) and *A. lentiformis* (big saltbush) constitute pair five. Both are included in a group of related woody dioecious shrubs by Hall and Clements (1923), and both have the evolutionary advanced C_4 mode of photosynthesis (Welkie and Caldwell 1970, Hatch et al. 1972), but they have distinctive floral and morphological differences (Brown 1956). The other chenopod pair (pair six), *Sarcobatus vermiculatus* (black greasewood) and *Ceratoides lanata* (winterfat), are probably the most loosely connected pair in the study. Both have C_3 photosynthesis (Welkie and Caldwell 1970), but are morphologically dissimilar. In fact, Standley (1916) placed greasewood closer to the saltbushes than to winterfat. The four rosaceous shrubs are all in the subfamily Rosoideae (Benson 1957). *Purshia tridentata* (antelope bitterbrush) and *Cowania mexicana* ssp. *stansburiana* (Stansbury cliffrose) comprise pair seven. Although placed in different genera, they are in fact closely related. Hybridization and introgression are common between the two species (Stutz and Thomas 1964, Blauer et al. 1975). The last pair (pair eight) was *Cercocarpus montanus* (true mountain mahogany) and *C. ledifolius* (curleaf mountain mahogany). This species pair is related closely enough to produce a number of interspecific hybrids (Blauer et al. 1975).

Seeds were obtained from native accessions and from transplanted shrubs maintained at the Snow Field Station at Ephraim, Utah (Table 1). Seedlings were germinated under greenhouse conditions in fine-textured sand within 15 cm plastic pots and kept moist throughout germination. Commercial fertilizer consisting of a basic nitrogen-potassium-phosphorus (20:20:20) composition (no micronutrients) was applied weekly, in solution, to seedlings following emergence. It was found that growing seedlings in sand permitted better drainage and aeration, with fewer problems with fungus and other pathogens than was evidenced with soil as a growth medium. Temperatures during growth ranged from approximately 18 to 25 C.

Plant material was used from three general stages of growth: seedling (to approximately 20 pairs of leaves), juvenile (from seedling stage to young plants starting to become woody, usually less than 30 cm in height), and adult plants (fully grown, from field or garden collection sites). Plants were consistently used from accessions listed in Table 1, to reduce intraspecific variation (one accession per species). Leaf tissue was used for all extractions, with care to exclude stem or petiole, dehydrated portions of leaves, and extraneous matter.

Experimental Methods

To estimate approximate protein loadings of the samples used in electrophoresis, protein assays were conducted in accordance with Bio-Rad Laboratories' technique (Bio-Rad 1979). Due to the small sample size used in the study (approximately ½ ml) adjustment of the protein concentration within samples was not practical. Both dry weight and protein determination were conducted on samples at each growth stage. Vertical polyacrylamide gel was selected for the investigation because of the availability of commercial preformed gradient gels, superior resolving ability, pore size range, and less fragile texture. Slab gels used also permitted better comparison of banding between samples than conventional tubular (disc) gels (Leaback 1976). Pharmacia polyacrylamide gradient gels (PAA 4/30) were used. These gels have a maximum polyacrylamide concentration of from 50,000 to 2 million daltons (Pharmacia 1978).

One hundred milligrams of fresh leaf tissue was carefully weighed and placed in small prechilled mortars in a tray of cracked ice. To each leaf sample, ¼ ml refrigerated (2 C) Tris-boric buffer solution, pH 8.4, was added (Pharmacia n.d.), composition 0.09 M Tris, 0.08 M boric acid, 0.93 g/l Na_2EDTA . Density was increased by adding ¼ ml of a 40 percent sucrose solution to prevent diffusion of the sample into the reservoir buffer (Kuhns and Fretz 1978). To protect the proteins and

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prevent formation of oxidation products, 3 μ l of 2-mercaptoethanol (Thioglycol), 2 mg of L-ascorbic acid, and 2 mg of polyvinylpyrrolidone (PVP) were added to each sample.

In developing electrophoresis and staining procedures suitable for application to western shrub taxa, several problems were encountered. One of these was caused by the high levels of monoterpenoids and phenolics found in several species selected (Kelley and Adams 1977, McArthur et al. 1979, and Welch and McArthur 1981). Phenolics can form complexes with proteins and become readily oxidized. To lessen the probability of this interaction, PVP was added to extractions with 2-mercaptoethanol and ascorbic acid to bind phenols, protect protein integrity, and reduce smearing (Montgomery and Sgarbieri 1975). An additional problem was encountered in keeping the electrophoresis buffer cold to prevent inactivation of enzymes, with resulting pattern distortion (Brewer and Sing 1970). A pumping system was improvised that circulated ice water from a sink through cooling coils surrounding the buffer vessel, maintaining the temperature within prescribed limits (<10 C). The fresh leaf tissue was ground with additives in a small mortar and pestle (after Brewer and Sing 1970) until the tissue was well macerated and the mixture appeared homogeneous. This mixture was then centrifuged at approximately 10,000 g for about 10 minutes. Supernatant was withdrawn with pasteur pipette and analyzed by electrophoresis.

The electrophoresis apparatus used throughout this study was a Pharmacia vertical gel electrophoresis apparatus, GE-4 II, with accompanying power supply EPS 400/500 and accessory items (Pharmacia 1978). The supernatant was loaded into wells of an equilibrated slab gel with a 10- μ l microsyringe. Gradient 4/30 gels (4 to 30 percent polyacrylamide concentration) were used for the study, due to having higher resolving power than conventional nongradient gels.

The gel was charged at 70 volts (v.) constant voltage for 20 minutes until the samples began to migrate into the gel. Electrophoresis was then carried out for 15 hours at

150 v. (constant voltage) with the surrounding buffer temperature maintained between 5 and 10 C. Following electrophoresis, the gels were stained either for total protein or for particular enzyme activity. Total protein staining procedure consisted of exposing gels to a 10 percent sulfosalicylic acid solution for 30 minutes, followed by approximately 90 minutes in a solution of Aniline Blue-Black (acid black 1), in 25 percent methanol, 10 percent acetic acid, and water (v,v,v). Destaining was done using the Pharmacia destainer GD-4 II with a solution of 25 percent methanol, 10 percent acetic acid, and water (v,v,v) for approximately 60 to 90 minutes until background stain was removed. To detect isoenzyme bands, a series of 14 enzyme recipes were used (Scandalios 1969, Shaw and Prasad 1970), with modifications listed in Table 2. Scandalios listed references designed for 10 percent acrylamide gels, necessitating changes in incubation periods to accommodate the 4–30 percent Pharmacia gels. Selection of enzyme stains was based on a review of success achieved in previous studies, availability of ingredients, and simplicity of technique.

Bovine serum albumin (BSA) was found to produce consistent banding patterns between runs when stained with total protein preparation and was subsequently used as a reference to operating conditions. Six bands resulted with BSA which, in 24 replications, produced standard mean errors (SE) of less than 0.4 mm. Because of this consistency between runs the migration distances are expressed in terms of millimeters of migration from origin. The BSA band, which migrated to approximately 59 mm, was densely stained and used for reference for migration rates for all isoenzyme and protein bands.

All banding patterns were scored on a light table for position and intensity. Distance to each band center from the top surface of the gel was noted, and bands were assigned a relative intensity value on a range from 1 (faint band) to 5 (darkly stained). When negatively stained bands were present, positions were recorded as for other bands and an intensity of "1" assigned. Data were compiled, using the 13 effective enzyme-staining recipes plus total protein, for each of the selected species at seedling stage (glutamic oxytransaminase

[GOT] was not effective). In addition, several enzyme stains (4 for juvenile plants and 5 for adult plants) plus total protein were applied to more mature plants so that pattern differences between growth stages could be compared. A minimum of three runs were made on each stage and plant species, and results compiled to produce an overall pattern of reproducible bands (Table 3). Banding data were clustered for percentage of similarity (*s*) between species, using the following formula:

$$s = \frac{C - .1x}{T}$$

where C represents the number of bands in common between taxa compared;
T represents the total of different bands present in either taxa, combined;
and x represents the absolute value of the sum of intensity differences of taxa.

A weighting factor of 10 percent (.1) was deducted from the similar bands with differences in band intensity. This method of comparison has been used by Whitney et al. (1968) and McArthur et al. (1978), but without a weighting factor. Whitney et al. suggest, however, that band intensity may have taxonomic significance.

TABLE 2. Enzyme banding characteristics used in evaluating 16 shrub species.

Enzyme	Pattern features	Taxa resolution value and enzyme consistency	Original source	Modifications
Peroxidase	Blurred banding	Fair/good	Shaw & Prasad 1970	Refrigeration time increased to 3 hours
Amylases	Faint; one band/taxa	Fair/good	Scandalios 1969	None
Esterases	One band/taxa	Fair/good	Scandalios 1969	Incubation time increased to 3 hours
Catalase	One band/taxa	Fair/good	Scandalios 1969	H ₂ O ₂ concentrated increased to 10 percent; incubation time increased to 3 hours
Alcohol dehydrogenase (ADH)	Negatively stained bands present	Good/good	Scandalios 1969	Incubation time increased to 3 hours
Malate dehydrogenase (MDH)	Negatively stained bands present	Fair/good	Scandalios 1969	Stained in dark
Glutamate dehydrogenase (GDH)	Stained bands present	Poor/good	Shaw & Prasad 1970 Mitton et al. 1979	Stained in dark
Glucose-6-PO ₄ dehydrogenase (G-6-PD)	Many bands (or none) present/taxa	Poor/fair	Shaw & Prasad 1970	Stained in dark
Acid phosphatase	One band/taxa	Fair/good	Scandalios 1969	Incubation time increased to 16 hours
Alkaline phosphatase	Two color bands present	Fair/good	Scandalios 1969	None
Leucine amino-peptidase (LAP)	Two color bands present	Fair/good	Scandalios 1969	Incubation time increased to 4 hours
Phosphoglucose isomerase (PGI)	Often blurred banding	Good/fair	Shaw & Prasad 1970	Stained in dark
Phosphoglucomutase (PCM)	Negatively stained bands present	Fair/fair	Shaw & Prasad 1970 Mitton et al. 1979	Stained in dark
Glutamic oxytransaminase (GOT)	Blurred; no recognizable banding characteristics	Poor/poor	Shaw & Prasad 1970	Used Fast Blue BB salt

TABLE 3. Isoenzyme positions and intensity for the 16 shrub species at the seedling stage.

Enzyme	Species and isoenzyme migration distance from origin (mm) ¹							
	Arab	Arfr	Art ^r	Arno	Chna ^a	Chpa ^a	Chli	Chvi
Peroxidase	49/2 55/3 62/3 65/5	49/2 55/2 62/2 65/3	55/2 62/1	52/2 62/1 65/3	52/4 54/3 58/1	52/4 54/3	55/2 62/1	52/1 54/1 58/3 60/4
GDH	24/3	24/3	24/3	24/3	24/3	24/3	24/3	24/3
MDH	23/1	23/1	23/1	23/1	23/1	22/1	24/1	22/1
PGI	23/1 30/1 38/2 47/3	23/1 30/1 38/2 47/3	23/1 30/1 38/2 47/3	23/1 30/1 47/3	20/1 24/3 32/1 48/3 52/3	20/1 24/1 32/1 48/3 52/3	20/1 24/1 32/1 48/3 52/3	20/1 24/1 32/1 48/3 52/3
Esterase	24/3	24/3	24/3	24/3	24/3	24/3	24/3	24/3
Catalase	21/3	21/3	21/3	21/3	21/3	21/3	21/3	21/3
ADH	23/3 69/1	23/3 74/1	23/3 50/1	23/3 50/1	22/3 50/1 72/1	22/3 50/1 60/1 70/1	22/3 67/1 70/1	22/3 53/1 67/1 70/1
LAP	23/3 51/3	23/3 51/3	23/3 53/3	23/3 53/3	23/3 51/3	23/3 51/3	23/3 51/3	23/3 51/3
Amylases	22/2	22/2	22/2	22/2	22/2	22/2	22/2	22/2
Alkaline Phosphatase	23/3 55/2	23/3 46/1 51/1	23/3 46/3 51/1	23/3 46/2	23/3	23/3	23/3 46/1	23/3 46/1
G-6-PD	9/1 12/1 17/1	7/1 9/1 13/1 18/2	7/1 8/1 10/2 13/1	6/1 7/1 9/2 13/2 18/2	8/2 9/2 12/2 14/2 20/1	8/2 9/2 12/2 14/2 20/1	8/1 9/2 13/2 20/2	8/2 9/2 11/2 14/2 20/1
PGN	23/2 47/3 63/4	23/2 47/3 63/4	24/2 47/3 63/2	24/2 47/3 63/2	25/2 31/2 48/3 63/2	25/2 31/2 48/3 63/2	25/2 31/2 48/3 63/2	25/2 31/2 48/3 63/2
Acid Phosphatase	24/3	24/3	24/3	24/3	25/3	23/3	23/3	25/3

¹Numbers expressed represent the migration distance in millimeters, followed by the intensity for each band, symbol designation for taxa are listed in Table 1.

Clustering of *s* values (Table 4) representing characteristic bands appears in Figure 1. The dendrogram in Figure 1 was constructed using a cluster analysis technique (McArthur et al. 1978). Stems of the dendrogram were tied together in descending order according to *s* value for all taxa being united above each union. Figure 2 illustrates patterns produced by seedling stage plant material when stained for specific enzyme activity.

RESULTS

Banding positions indicated in Tables 3 and 5 illustrate and confirm the more similar relationships anticipated within pairs of species and within genera than within families, and greater similarity of species within families than between family groupings. Figure 1 illustrates the relationships found between taxa. Of the enzyme stains used during the study for taxa differentiation, several were superior, namely, alcohol dehydrogenase

(ADH), phosphoglucose isomerase (PGI), and phosphoglucomutase (PGM), in the number of bands present, resolution value, and consistency (Table 2). Others were also productive but offered less distinction between taxa.

Variability in banding patterns may be representative of age (Whitney et al. 1968) or environmental variation (Pandey 1967, Latner and Skillen 1968, Myers 1978). Differences in banding were noted between stages of growth, but not in a predictable manner. Clusters assembled from enzyme banding patterns at later growth stages were similar to those found within seedling stage plants in most cases. Juvenile stage shrubs clustered consistently within pairs, genera, and families. Adult plants did so, too, except for separation at the genus level of two *Artemisia* species and at the family level of the *Atriplex* species. In both more mature stages, the level of clustering between taxa was generally lower. Much of this difference may have

Table 3 continued.

Enzyme	Species and isoenzyme migration distance from origin (mm) ¹							
	Atca	Atle	Save	Cela	Putr	Come ^s	Cemo	Cele
Peroxidase	32/2	37/2	44/1 54/1	54/1	47/1	38/1 44/1 52/2	44/1 55/1	—
GDH	—	—	22/1	22/1	22/1	22/1	22/1	22/1
MDH	25/1	25/1	20/1	22/1 37/1	23/1	23/1	23/1	23/1
PGI	51/5 53/2 55/2	51/5 53/2 55/2	51/2	45/3 51/2	45/1 49/1	45/1 49/1	45/1 49/1	45/1 49/1
Esterases	—	—	—	—	22/2	—	—	—
Catalase	—	23/1	20/3	23/1	23/3	23/3	23/3	23/3
ADH	23/1 61/1	23/1 37/1 56/1 72/1	21/3 58/1	—	23/1	23/1	23/1	—
LAP	21/3 55/2	21/3 55/2	22/1 55/1	19/1 55/1	21/1 55/2	21/1 55/2	21/1 55/2	21/1 55/2
Amylases	—	25/1	22/2	—	23/1	23/1	23/1	—
Alkaline Phosphatase	—	24/2 50/1	21/2 50/1	—	23/2	23/2	23/2	23/2
G-6-PD	—	—	—	—	—	—	—	—
PGC	58/1 52/3 63/3	48/3 52/3 63/3	38/1	45/2 49/2 63/1	44/1 49/3 53/2	48/3	42/1 51/3	42/1 51/3
Acid Phosphatase	27/1	27/1	—	—	24/2	24/2	24/2	24/2

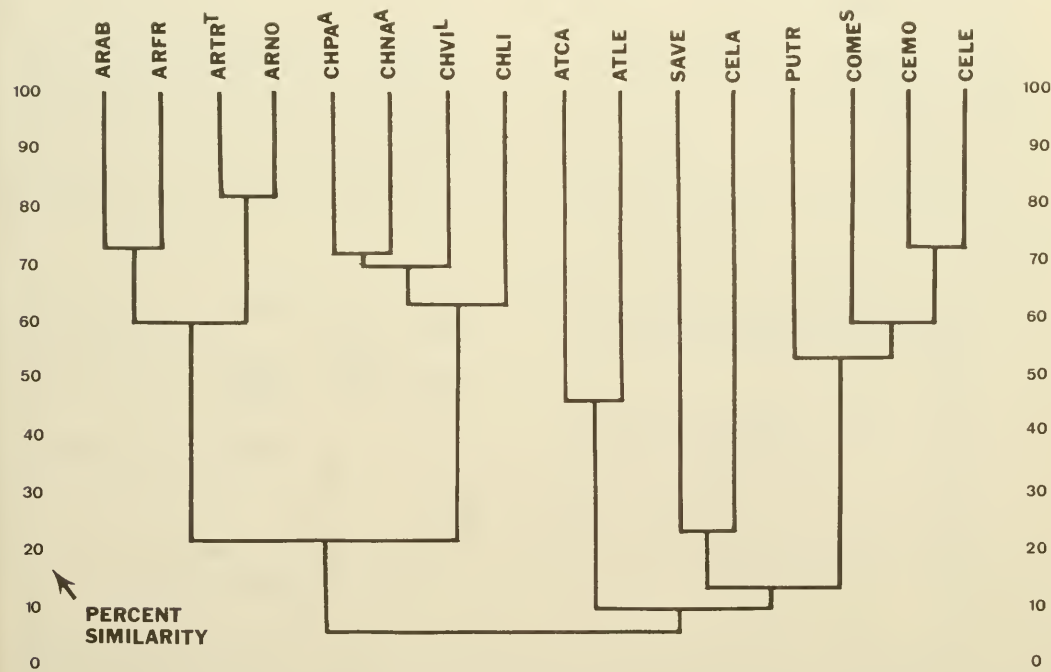


Fig. 1. Dendrogram of 16 shrub species based on similarity (s) value. (Symbol designations for taxa are listed in Table 1.)

been due to fewer enzyme systems used in their analysis.

Percentage dry weight of fresh leaf tissue ranged from approximately 30 to 80 percent, depending on taxa and stage of growth. Morrison (1961) stated that winterfat (*Ceratoides lanata*) possesses approximately 65 percent total dry matter, sagebrush leaves approximately 50 percent dry matter, and saltbush 28 percent dry matter. This study confirmed these findings, with adult basin big sagebrush and black sagebrush averaging 45 percent dry weight; big saltbush 35 percent, and winterfat 63 percent.

Protein concentrations using the Bio-Rad technique varied between approximately 1.1 mg/ml and 2.0 mg/ml at the seedling stage (depending on taxa). Several of the selected taxa displayed increases in protein levels upon maturation.

DISCUSSION AND CONCLUSIONS

The cluster analysis of seedling materials showed similarities between all but two of the proposed species pairs (Table 1, Fig. 1). The two exceptions were the mountain low rabbitbrush-spreading rabbitbrush and the bitterbrush-cliffrose pairs. In the rabbitbrush case, the two species have an *s* value of 66 percent (Table 4), but the low rabbitbrush clusters slightly closer (*s* = 70) to the two *Nauseosi* species. Spreading rabbitbrush has an *s* value (66) more similar to that of low rabbitbrush than do the other two rabbit-

brush species (*s* = 58 and 65). All the rabbitbrushes together cluster at a high level (*s* = 67). The other exception (bitterbrush-cliffrose) to the proposed pairs occurs because cliffrose clusters more tightly with true mountain mahogany (*s* = 67) than it does to bitterbrush (*s* = 55). The cliffrose *s* value with curleaf mountain mahogany is 53. Although cliffrose is considered to be allied closer to bitterbrush than to the mahoganies (Stutz and Thomas 1964), it shares with the mahoganies the floral characteristic that bitterbrush lacks, namely, persistent plumed styles (Blauer et al. 1975).

The *Artemisia* pairs cluster in each subgenus at *s* values > 70. *Artemisia* and *Chrysothamnus* are in different composite tribes, *Anthemideae* and *Astereae*, respectively. Our cluster diagram (Fig. 1) supports their within-family relationship.

The chenopod pairs both clustered as anticipated. The saltbush pair has an *s* value of 46 (Table 4, Fig. 1). These saltbushes have affinities in photosynthetic pathways and shrubby habit (Welkie and Caldwell 1970), but contrasts in floral, fruit, and leaf characteristics (Hall and Clements 1923, Brown 1956). Greasewood and winterfat have the lowest *s* value (17) of all pairs. This low value is consistent with Standley's (1916) placement of them in separate subfamilies. Both were distant enough from the saltbushes that they clustered more closely with the rose family shrubs. We found it interesting that there was some isoenzyme similarity across

TABLE 4. Percent similarity of isoenzyme bands for 16 shrub species—seedling stage.

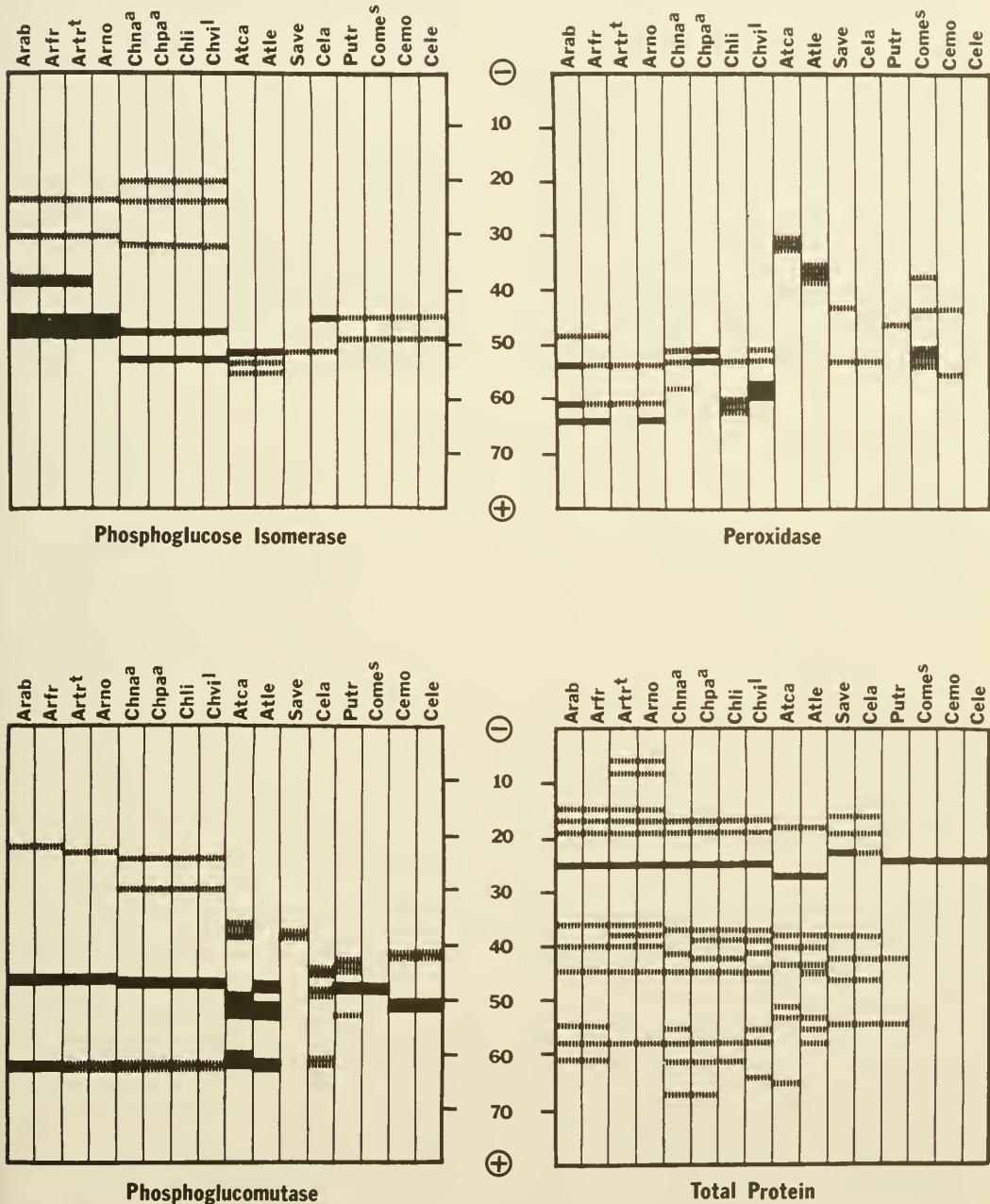
Taxa ¹	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 Arab															
2 Arfr	73														
3 Artr ^d	49	64													
4 Arno	52	72	83												
5 Chpa ^a	23	18	19	19											
6 Chna ^a	24	21	22	22	72										
7 Chvi ⁱ	17	20	17	18	68	71									
8 Chli	21	27	27	25	65	58	66								
9 Atca	4	4	4	4	2	2	2	2							
10 Atle	4	4	4	4	4	6	4	4	46						
11 Save	2	2	2	2	4	5	4	5	11	9					
12 Cela	2	2	2	2	7	5	7	5	10	8	17				
13 Putr	9	9	9	9	2	4	2	2	3	9	7	18			
14 Come ^e	10	10	10	10	6	10	6	5	11	13	11	15	55		
15 Cemo	12	12	12	12	2	4	2	2	11	9	11	15	55	67	
16 Cele	8	8	8	8	2	5	2	2	8	6	8	18	50	53	73

¹Symbol designations for taxa are listed in Table 1.

all 16 of these diverse shrub species (Fig. 1, Table 4).

In an earlier study (McArthur et al. 1978), comparisons of similarity among some of the

same *Chrysothamnus* taxa were reported by comparing phenolic compounds. With isoenzymes (this study), the overall rabbitbrush average *s* value was 67 compared to 42 with



Legend:
lightly stained bands
more densely stained bands

Fig. 2. Zymograms of selected isoenzymes and total protein for 16 shrub species. (Symbol designations for taxa are listed in Table 1.)

the phenolic compounds. It may be significant that isoenzymes are biosynthetically closer to their DNA encoders than are phenolics (Wagner and Mitchell 1964).

Polyacrylamide gel electrophoresis offers several distinct advantages as a technique for investigating genetic or evolutionary relationships among taxa of interest. The preformed gradient gels eliminate the time of preparation and exposure to toxic unpolymersized acrylamide. Gradient concentration with corresponding variations in pore size permits a sieving effect that tends to sharpen and accentuate differences in isoenzyme mobility (Brewer and Sing 1970, Leaback 1976). This separation assists in characterizing closely related taxa. The results of this study using morphologically distinct taxa will permit fur-

ther studies on narrower, taxonomically difficult shrub groups. The results also point out the opportunity for studies designed to gain better understanding of the breeding systems and population genetics of *Artemisia*, *Chrysothamnus*, *Atriplex*, *Ceratoides*, *Sarcobatus*, *Purshia*, *Cowania*, and *Cercocarpus*.

ACKNOWLEDGMENTS

This paper was part of the requirement for an M.S. degree for the senior author in the Department of Botany and Range Science at Brigham Young University. The work reported here was facilitated by a cooperative agreement between the Intermountain Forest and Range Experiment Station and Brigham Young University #12-11-204-26, an ASBYU

TABLE 5. Protein band positions within 16 shrub species¹—seedling stage.

Bovine serum albumin 1.0% solution ²	Species and migration						
	Arab	Arfr	Artr ⁴	Arno	Chna ^a	Chpa ^a	Chli
			6	6			
			8	8			
	15	15	15	15			
	17	17	17	17	17	17	17
23.2 ± 0.3 n = 24	25	25	25	25	25	25	25
28.5 ± 0.3 n = 24							
34.4 ± 0.3 n = 24	36	36	36	36	37	37	37
			38	38		39	39
	40	40	40	40	41	41	42
44.0 ± 0.4 n = 26	45	45	45	45	45	45	45
	55	55			55		
58.8 ± 0.4 n = 26	58	58	58	58	58	58	58
	61	61			61	61	61
66.7 ± 0.4 n = 25					67	67	

¹Symbol designations for taxa are listed in Table 1.
²A 1.0 percent solution of bovine serum albumin produced 6 characteristic bands with position, standard mean of the error, and sample size (n) as shown. These bands were used as a reference for consistency.

Student Research Fund Grant, and the Utah Division of Wildlife Resources Pittman Robertson Project W-82-R. The authors thank Drs. D. Duffield, D. L. Nelson, H. C. Stutz, A. R. Tiedemann, R. K. Vickery, and B. L. Welch, and Mr. R. B. Ferguson for technical advice.

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Table 5 continued.

distances from origin (mm)								
Chvi ¹	Atca	Atle	Save	Cela	Putr	Come ⁵	Cemo	Cele
17			16	16				
	18	18	19	19				
			23	23				
					24	24	24	24
25								
	27	27						
37								
	38	38	38	38				
39								
	40	40						
42			42	42	42			
	43	43						
45		45						
			46	46				
	51							
	53	53						
			54	54	54			
55		55						
58		58						
64								
	65							

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NEST OF *FORMICA PROPINQUA* (HYMENOPTERA:FORMICIDAE)

George C. Wheeler¹ and Jeanette Wheeler¹

ABSTRACT.— The nest of the ant *Formica propinqua* W. M. Wheeler is reported from Washoe Co., Nevada.

Little Valley is in the Carson Range, which, according to Fenneman (1931:402), is a subordinate range of the Sierra Nevada, "an uplifted block between parallel faults, a separate range from the Sierra Nevada but included in the same physiographic section. Lake Tahoe occupies the 'moat' between the fault scarps of the main Sierra and Carson Ranges."

Whittell Forest, which is practically coextensive with Little Valley, is a biological research area owned by the University of Nevada at Reno. The legal description places it in T 16 N, R. 19 E., sections 5, 8, 17, 18, 19, 20, in Washoe County, Nevada.

Our study site is in the SW $\frac{1}{4}$ of section 17, about 4 miles east of Lake Tahoe and 20 miles south of Reno. It is in a second-growth pine forest. The range was denuded of its virgin forest after the silver rush of 1859: our site is only 12 miles from Virginia City with its Comstock Lode. A few huge stumps are evidence of the original cover, even after 140 years.

The site is an open portion of a forest of Jeffrey pine (*Pinus jeffreyi*) and lodgepole (*P. contorta*), which is mostly surrounded by dense forest. We staked out in 50 foot squares an area totaling 2.7 acres (= 1.1 hectare). On the area there were 210 lodgepole (range 1–34 inches DBH, average 16.6 and median 15 inches) and 27 Jeffrey (range 1–36 inches DBH, average and median 19.8 inches).

In this area we found 35 nests of *Formica propinqua*. We numbered each nest, photographed it, and plotted it on the map. This gives an average of 13 nests per acre (= 32 per hectare). We did not find this species anywhere else in the forest. In fact, although we have it at several localities in Nevada and

California, we have never seen so many nests in such a small area.

The nests were always in the open, where they were fully exposed to the sun for at least part of the day. We never found them in full shade and hence never in the dense forest.

A nest was always associated with solid dead wood. It could be in or under a prostrate trunk (even a trunk several feet above the ground), in or around a stump, or along a mere slab; the wood might be decayed inside but at least a part of the outside was solid.

The shape of the nest mound was highly variable; we never found two alike; the ants were highly opportunistic in this respect. This is in sharp contrast to certain other members of the *rufa* species-group of *Formica*, which typically construct neat paraboloidal domes. The accompanying photographs illustrate this variability in *F. propinqua*.

The nest material comprised pieces of plant stems about one inch long. These are mixed with smaller plant debris, decayed wood, and soil. In other words, again this species differs from some of its *rufa* relatives, which build typical neat mounds of one or a few kinds of longer pieces of plant materials, e.g., sagebrush twigs, grass culms, pine needles or juniper sprays. In short, the nest mounds of *propinqua* are messy.

THE ANTS

It would be very interesting to know the population of this entire community. Speculation leads us to think in millions; but it is so easy to underestimate or overestimate an ant population and so difficult to get an actual census, let us be content with *enormous*.

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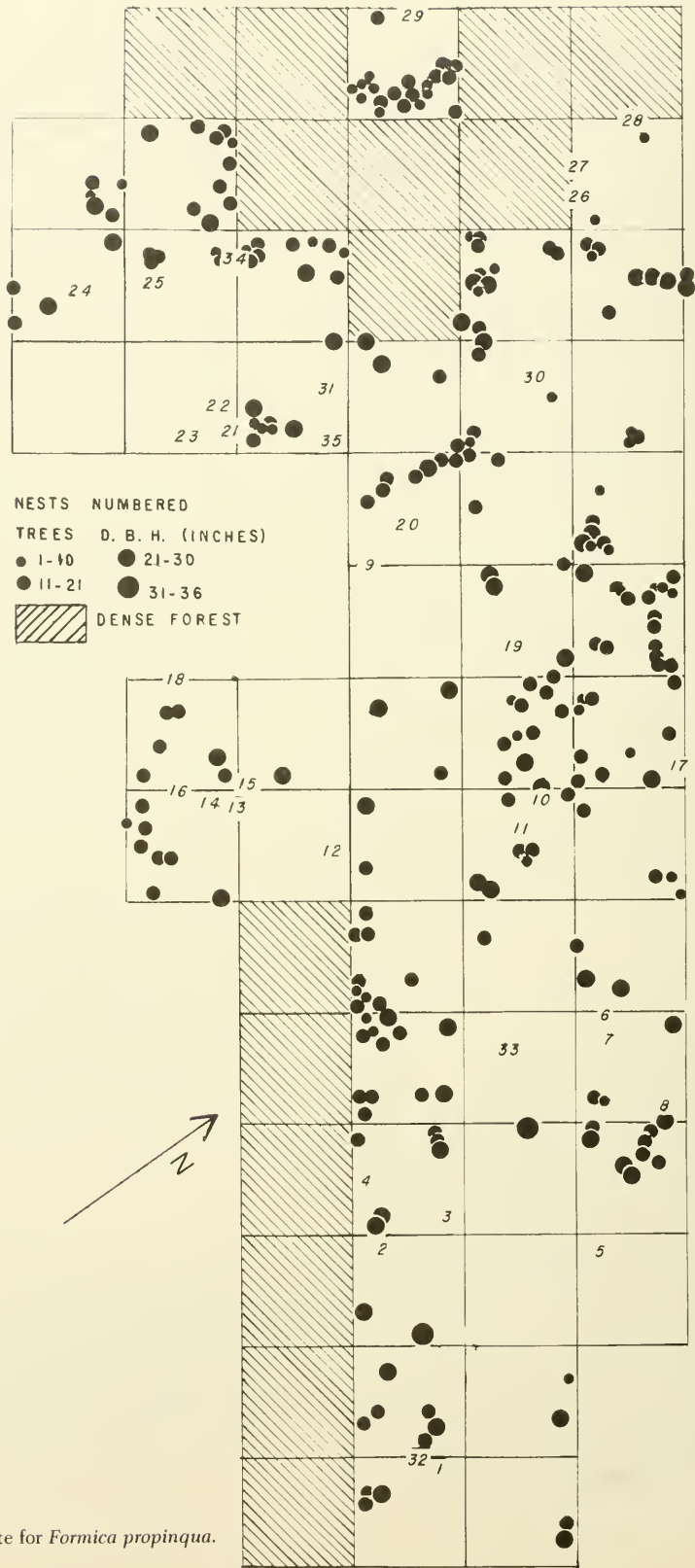


Fig. 1. Map of study site for *Formica propinqua*.



Fig. 2. Photographs of 9 tatch mounds of *Formica propinqua* in the study area.

This leads immediately to the question what is the food supply for such a population? There were not enough other insects (even including the small colonies of other ant species). We found *propinqua* workers tending aphids on pine needles. There were certainly enough aphids to support an enormous ant population. In addition to the honeydew the aphids secrete, the ants could eat some of the aphids for their protein supply.

In some respects the workers of *propinqua* were like their congeners: they were active and aggressive; their bite was annoying and when disturbed they were quick to becloud the atmosphere with formic acid.

EPILOGUE

The above observations were made in 1968. We were ready to continue the study, investigating such topics as population, poly-

caly and food supply, but our interests were diverted for 10 years. In 1978 we decided to resume the study and revisited the study area. After a prolonged search we found a few moribund nests. What had happened? To be sure, the trees had grown considerably, but there was still ample open space for many nests. The cause of the population crash must remain a myrmecological mystery.

It is interesting to note here that we had previously found in other parts of Little Valley high concentrations of *Manica bradleyi* and *Formica sybilla*. They, too, suffered a population crash (see Wheeler and Wheeler 1970).

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RANGE EXTENSION OF *HELIANTHUS* SPP. (*ASTERACEAE*) IN ARIZONA AND UTAH¹

Gerald J. Seiler² and Luka Cuk³

ABSTRACT.— Two populations of *Helianthus niveus* (Benth.) Brandege ssp. *canescens* (A. Gray) Heiser were discovered in northern Arizona extending the range 300 miles north for this species. *Helianthus deserticola* Heiser range was extended 100 miles east in both Arizona and Utah.

Recent explorations for *Helianthus* species for a germplasm resource collection during the summer of 1980 led to several new distribution records. Range extensions were discovered for *Helianthus niveus* (Benth.) Brandege ssp. *canescens*, (A. Gray) Heiser and *H. deserticola* Heiser.

Helianthus niveus ssp. *canescens* was listed as occurring in southern Arizona (Kearney and Pebbles 1960). McDougall (1973) did not list this species as occurring in northern Arizona. During our explorations we located two populations in northern Arizona, one in a sandy roadside ditch 4 miles northeast of Mexican Water, Apache Co., 29 Sept. 1980, Seiler and Cuk 1496, and the other in sandy soil 21.5 miles northeast of Kayenta, Apache Co., 29 Sept. 1980, Seiler and Cuk 1498. Both populations were small and scattered, and plants were shorter than usual. These collections represent a northern extension of about 300 miles in Arizona.

Heiser et al. (1969) listed the distribution of *H. deserticola* as southwestern Utah, southeastern and west central Nevada, and the extreme northwestern corner of Arizona. Welsh et al. (1973) and Welsh (1978) listed *H. deserticola* as a candidate threatened species, being restricted to sand dunes in Washington Co., Utah. McDougall (1973) did not list this species as occurring in northern Arizona. We found a very large population extending for several miles on both sides of the highway and extending into adjacent fields in sandy soil beginning 7.5 miles northwest of Page, Coconino Co., Arizona, 28 Sept. 1980, Seiler

and Cuk 1485. This collection represents an eastern extension of 100 miles for this species in Arizona. One other large population of *H. deserticola* was found in sandy soil in south-central Utah, 2 miles west of Glen Canyon, Kane Co., 28 Sept. 1980, Seiler and Cuk 1484. This collection represents an eastern extension of 100 miles for this species in Utah.

Specimens cited are deposited at the herbarium of the United States Department of Agriculture, Agricultural Research Service, Conservation and Production Research Laboratory, Bushland, Texas.

ACKNOWLEDGMENTS

We thank the Southern Regional Plant Introduction Station, Germplasm Institute, USDA-ARS, for a grant providing funds to make these field studies possible. We also thank Dr. Charles B. Heiser, Jr., Indiana University, Bloomington, Indiana, for verification of specimens.

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SPECIES COMPOSITION AND RELATIVE ABUNDANCE OF ADULT FISH IN PYRAMID LAKE, NEVADA

Steven Vigg¹

ABSTRACT.— Pyramid Lake fish populations were sampled with nets on a monthly basis from November 1975 through December 1977. Fish species were taken in the following order of numerical relative abundance: tui chub (*Gila bicolor*), Tahoe sucker (*Catostomus tahoensis*), Lahontan cutthroat trout (*Salmo clarki henshawi*) including cutthroat-rainbow hybrids, cui-ui (*Chasmistes cujus*), and Sacramento perch (*Archoplites interruptus*). Relative abundance estimates are discussed with respect to seasonal availability, spatial distribution of the fish, sampling bias of the fishing methods, and biomass of the fish. Recent temporal trends in the population structure of the lake are presented.

In fisheries biology a basic measure of abundance is catch-per-unit-effort, or stock density (Cushing 1968). Catch/effort (C/f) is nearly always the best available measure of the true stock density, although rarely exactly proportional (Gulland 1969). Marr (1951) termed relative abundance as determined by C/f measurements as "relative apparent abundance." Passive fishing gear such as trap and gill nets are standardly used to sample fish populations as a practical necessity because more direct methods (e.g., seining, poisoning, and mark-recovery techniques) frequently are not applicable to large natural lakes (Moyle 1950). Extensive use of gill nets over the entire growing season generally provides the best estimate of species composition, size composition, and relative abundance of lake fish populations (Powell et al. 1971, Walberg 1969).

Fish of different sizes may be caught with varying efficiency, either as a result of selectivity of fishing gear or because of differences in distribution or habitat; thus, as fish grow their vulnerability to capture changes (Ricker 1958). Therefore, it may be advisable to use two or more types of gear in estimating fish population statistics. After evaluating C/f data, Walberg (1969) concluded that trap and gill nets were most efficient for sampling adult fish. Similarly, Yeh (1977) found small hoop nets used in conjunction with gill nets to be the most efficient paired gear to

estimate species composition and relative abundance.

The purpose of this research was to estimate the relative abundance of fish populations in Pyramid Lake, taking into account the reliability of the estimate with respect to inherent sampling biases. A valid relative abundance estimate of fish populations is contingent upon the representative sample on which the estimate is based; i.e., it must equal the proportion of the species in the lake. All fish sampling methods have inherent biases, however, due to interactions with fish size, distribution, habitat preference, behavior, or physical characteristics, which in turn are a function of species, age, and environmental conditions.

To obtain a valid estimate of species composition and relative abundance in Pyramid Lake, several sampling methods were used in various habitat types. Three comparative perspectives are presented (i.e., catch statistics derived from):

1. Bottom-set gill net samples stratified by depth and area during a two-year period; these data are also related to comparable historical data.
2. Four independent passive and active fishing methods, i.e., gill nets, fyke nets, beach seines and otter trawls.
3. Six distinct habitat types utilizing three different but comparable gill net fishing methods; data are weighted according

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to the proportion of the total lake volume that each habitat represents. These data are also transformed into biomass estimates.

STUDY AREA

Pyramid Lake is the terminal water body of the endorheic Truckee River system that originates some 192 river km upstream at Lake Tahoe. Pyramid Lake is about 40 km long, with a north-south axis; its width varies from 16 km at the north to 6.5 km at the south. During 1976, the mean elevation was 1,157.3 m above sea level, corresponding to a surface area of 446.4 km², volume of 26.4 km³, mean depth of 59 m, and maximum depth of 103 m (United States Geological Survey 1977, Harris 1970).

The only outflow from Pyramid Lake is by evaporation. Due to water diversions from the Truckee River, the water level of Pyramid Lake has declined 22 m since 1909. The lake water is highly ionic, being saline and alkaline with a pH of 9.2. The 1976 total dissolved solids concentration was 5,235 mg/l.

During 1976 and 1977 mean surface temperature ranged from 6.1 to 23.1 C. As winds subside and surface water temperature increases, a thermocline is formed from June through December. The lake is monomictic, turnover begins in early winter, and mixing extends to spring.

PROCEDURES

Three east-west sampling transects were selected in Pyramid Lake that are representative of the north, middle, and south sections (Fig. 1). Four gill net stations were established along each transect, i.e., onshore and offshore on the east and west sides of the lake. I activated this sampling design in November 1975 and conducted it through December 1977. A fifth sampling station, representing a specialized habitat, was established beginning February 1976 in each section, i.e., north: Pinnacles thermal springs; middle: profundal; and south: Truckee River delta. Gill nets were set during the first week of each month at each of the 15 sampling stations. Variable-mesh, bottom-set gill nets were utilized. The 1.83 × 76.20 m gill nets

were composed of ten 1.83 × 7.62 m panels of the following mesh sizes (cm bar measure): 1.27, 1.91, 2.54, 3.18, 3.81, 4.45, 5.08, 6.35, 7.62, and 8.89. The nets were built of white multifilament nylon of the following thread diameters (for respective mesh sizes): 0.23 mm (1.27 cm), 0.28 mm (1.91 and 2.54 cm), 0.33 mm (3.18, 3.81, 4.45, 5.08 and 6.35 cm), and 0.40 mm (7.62 and 8.89 cm). A total of 373 gill net sets were made during the standardized monthly sampling program.

Supplemental sampling was conducted at various depths with the standard bottom-set gill nets. During September and December 1976 and March and June 1977, 52 bottom gill net sets were made in the profundal zone of Pyramid Lake at depths exceeding 61 m (Vigg 1980). The net sets were stratified on an areal basis within the benthic profundal zone. This sampling program further defined relative abundance of fish species with respect to bottom depths and associated environmental parameters.

In addition, five other gear types were used: surface gill nets, vertical gill nets, fyke nets, beach seines, and otter trawls. These ancillary fishing methods were utilized to obtain samples representative of all major habitat types and to facilitate evaluation of gear bias.

Vertical distribution was evaluated inshore with paired surface-bottom gill nets, and offshore with vertical gill nets (Vigg 1978). Variable mesh, surface-set gill nets were utilized to sample inshore relative fish abundance above the thermocline in conjunction with standard bottom-set gill nets below the thermocline at 23 m. The 76.20 m long surface gill nets were identical to the standard, bottom-set nets except they were 3.66 instead of 1.83 m deep and rigged to float on the surface instead of sinking to the bottom. Surface gill nets were test fished from February through May 1977 (12 samples) in conjunction with the primary monthly netting program. An intensive monthly surface-bottom netting program was implemented from June through November 1977. During this period, 35 surface samples above the thermocline and 35 bottom samples below the thermocline, at a depth of 23 m, were taken. These surface-bottom samples at 23 m were

stratified by lake area along the same transects used in the primary gill netting program.

Vertical gill nets similar to those described by Horak and Tanner (1964) were utilized to study limnetic relative fish abundance. The

nets, 2.44×45.72 m, were set overnight in gangs of eight nets of the following mesh sizes (cm bar measure): 1.27, 1.91, 2.54, 3.81, 5.08, 6.35, 6.62 and 8.89. Spreader bars physically separated each net into six 7.62 m

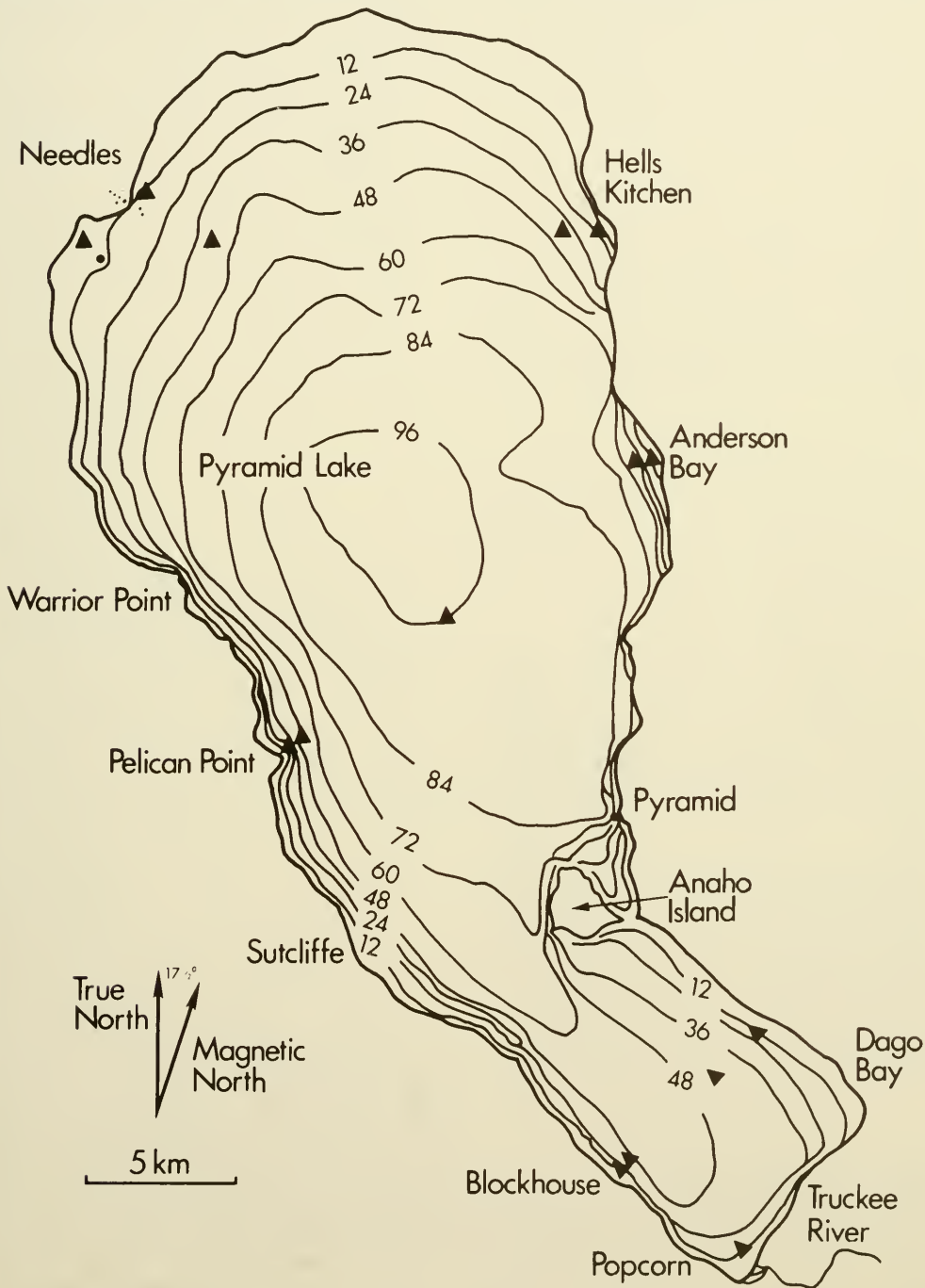


Fig. 1. Sampling stations in Pyramid Lake, Nevada.

depth increments. From December 1975 through February 1976 four large mesh vertical gill nets were test fished in offshore areas; however, bad weather made the netting inefficient and the catch rate was very low, apparently due to the large mesh sizes utilized. I implemented an intensive vertical gill netting program from June through October 1977. A total of 18 sets of gangs of eight vertical gill nets were made at a midlake limnetic station during the period on a monthly basis.

Fyke nets were set at six stratified onshore stations in conjunction with the monthly gill net samples. They were constructed of 1.27 cm bar mesh nylon netting covering four 1.22 m diameter fiberglass hoops. The extended net was 4.88 m in length with a 15.24 m lead that was set perpendicular to shore. A total of 147 fyke net sets were made on a monthly basis.

A 121.92 m beach seine (77 samples) and a 4.87 m bottom otter trawl (63 samples) were utilized in stratified lake areas from November 1975 to November 1976 on a seasonal basis. The 121.92 m beach seine with a 3.05 m deep bag of 1.27 cm bar mesh was fished in shallow areas of suitable substrate on the west shore of the lake. The seine was operated by setting it parallel approximately 30 m from shore with a small boat, then simultaneously pulling both ends of the net to shore. The 7.62 m semiballoon otter trawl with a 0.64 cm bar mesh interliner was fished on the bottom, throughout the lake, at depths up to 46 m.

Species composition was determined from the fish caught in all types of sampling gear. Relative abundance was estimated from catch statistics derived from each sampling method separately and all sampling gears combined. Relative abundance was also analyzed with respect to discrete habitat types and the proportion of the lake represented by each habitat.

RESULT AND DISCUSSION

The historical fish species composition of Pyramid Lake, original and introduced, is listed in Table 1. Ten species were captured during 1975–1977; the five most abundant species composed over 99.9 percent of the

total catch. Tui chub was clearly the predominant species, followed in numerical relative abundance by Tahoe sucker, Lahontan cutthroat trout, cui-ui, and Sacramento perch. During this study we captured over 73,000 fish with nearly 800 net samples, utilizing six different fishing methods in a variety of habitat types (Table 2).

This catch tabulation may be considered a relative abundance estimate in itself; however, consideration of three factors is necessary for the valid interpretation of these data. Sampling bias, temporal, and spatial factors are interactive and must be weighted with respect to the ecology of the fish populations in Pyramid Lake.

Any single fishing method can introduce bias by providing a sample that is not representative of the true population. Comparison of two or more sampling methods enables at least a partial dealing with this problem. Juveniles are generally not captured in proportion to their actual abundance because their vulnerability to capture increases as they grow and the actual population size undergoes drastic changes during the first year of life. This problem is largely eliminated by ignoring the dynamic juvenile population and obtaining an index of only the adult population. Each population has a species-specific temporal activity pattern within the year. To obtain a representative sample of all species present in a lake, the sampling period must include the active season of each species. Therefore, the minimum time frame is the growing season for the fish; however, monthly sampling throughout the year is desirable to insure inclusion of the entire annual activity cycle for each species. In Pyramid Lake, the fish populations exhibit marked changes in vertical and benthic spatial distribution (Vigg 1978, 1980). For the cutthroat trout and tui chub populations, these distribution patterns interact with temporal activity cycles. Thus, various vertical and horizontal strata must be sampled to obtain a realistic sample of relative fish abundance. Pyramid Lake is a large, deep body of water with heterogeneous and discrete habitat types. The limnetic zone especially requires adequate representation in fish sampling because the offshore water column comprises over half

the total volume of Pyramid Lake. Furthermore, a morphologically distinct planktivorous population of tui chubs exists in the limnetic zone of Pyramid Lake, in contrast to the benthic inshore form.

Although conventional fishing methods utilized in this research do not guarantee a sample that is exactly proportional to the

true population in Pyramid Lake, consideration of the previously mentioned factors enables quantitative estimates of relative abundance. I derived three comparative estimates of relative abundance from the fish catch data (Table 3). Although it is impossible to determine which one, if any, represents the true proportion of fish populations

TABLE 1. Original and introduced fish fauna of Pyramid Lake, Nevada (after La Rivers 1962 and U.S. Department of the Interior 1975).¹

Fish species	
Common name	Scientific name
ORIGINAL SPECIES	
°Lahontan cutthroat trout	<i>Salmo clarki henshawi</i> ²
Pyramid rainbow trout	<i>Salmo gairdneri smaragdus</i> ³
°Cui-ui	<i>Chasmistes cujus</i> ⁴
°Tahoe sucker	<i>Catostomus tahoensis</i>
Mountain sucker	<i>Catostomus platyrhynchus</i> ⁵
°Lahontan redbside	<i>Richardsonius egregius</i> ⁶
°Lahontan tui chub	<i>Gila bicolor (obesa and pectinifer)</i> ⁶
°Lahontan speckled dace	<i>Rhinichthys osculus robustus</i> ⁶
INTRODUCED SPECIES	
Kokanee	<i>Oncorhynchus nerka kennerlyi</i>
Coho salmon	<i>Oncorhynchus kisutch</i>
Rainbow trout	<i>Salmo gairdneri</i> ⁶
Brown trout	<i>Salmo trutta</i>
Yellowstone cutthroat trout	<i>Salmo clarki lewisi</i>
°Cutthroat trout hybrids	
Cuttbow: male cutthroat × female rainbow	
Bowcutt: Male rainbow × female cutthroat	
Kamcutt: Male Kamloops rainbow × female cutthroat	
Brook trout	<i>Salvelinus fontinalis</i>
°Carp	<i>Cyprinus carpio</i>
Channel catfish	<i>Ictalurus punctatus</i>
Bluegill	<i>Lepomis macrochirus</i>
°Sacramento perch	<i>Archoplites interruptus</i>
INTRODUCED RESIDENT SPECIES IN THE LOWER TRUCKEE RIVER WITH ACCESS TO PYRAMID LAKE	
°Mosquitofish	<i>Gambusia affinis</i>
Black bullhead	<i>Ictalurus melas</i>
Brown bullhead	<i>Ictalurus nebulosus</i>
°Largemouth bass	<i>Micropterus salmoides</i>
Green sunfish	<i>Lepomis cyanellus</i>
Black crappie	<i>Pomoxis nigromaculatus</i>
NATIVE TO THE UPPER TRUCKEE RIVER, PROBABLY WITHOUT ACCESS TO PYRAMID LAKE	
Mountain whitefish	<i>Prosopium williamsoni</i>
Paiute sculpin	<i>Cottus beldingi</i>

°Captured in Pyramid Lake during 1976–1977.

¹Nomenclature after Bailey et al. (1970) except for subspecies.

²The original strain of Pyramid Lake Lahontan cutthroat trout is believed to have become extinct in the 1940s. Nevertheless, strains of Lahontan cutthroat trout (Heenan Lake, Walker Lake, and Summit Lake) that are remnants of the original Pyramid Lake strain have been reintroduced into Pyramid Lake. Hickman and Behnke (1979) may have recently discovered a population exhibiting the genetic composition of the original strain.

³Not a good taxonomic unit, possibly an early introduction of rainbow trout or an atypical Lahontan cutthroat trout (La Rivers 1962).

⁴Officially considered an endangered species; occurs only in Pyramid Lake.

⁵Previously *Pantosteus lahontan*, *Pantosteus* was reduced to a subgenus of *Catostomus* (Bailey et al. 1970).

⁶Two forms of Lahontan tui chub are known to exist, i.e., *Gila bicolor obesa* (Girard), which is characterized by coarse gill rakers, and *Gila bicolor pectinifer* (Snyder), which exhibits fine gill rakers. Disagreement exists among authorities whether or not these forms represent discrete taxons. Miller (1951) and Hopkirk and Behnke (1966) consider the two forms to be distinct species. Hubbs, Miller, and Hubbs (1974) consider the two types to be subspecies that exhibit intraspecific intergradation, and La Rivers and Trelease (1952) state that *G.b. pectinifer* is not a valid taxon. Kimsey (1954) considers the tui chub population occurring in Eagle Lake best described by the scientific name *bicolor: obesa* × *pectinifer*. A further taxonomic complication exists because *Gila bicolor* are known to hybridize with *Richardsonius egregius* and *Rhinichthys osculus* in Lake Tahoe (Evans 1969).

⁷Pen culture of coho occurred before and during this study.

⁸Including steelhead and kamloops strains.

⁹Questionable species that may fit into this category include: Yellow perch, White crappie, White catfish, and Sacramento blackfish.

of Pyramid Lake, in the following sections I will discuss the relative merits of the estimates derived from:

- 1. Bottom-set gill nets
- 2. Four independent sampling methods
- 3. Six habitat types

Bottom-Set Gill Nets

It is generally recognized that variable-mesh gill nets provide the best single estimate of population statistics for lacustrine

fish. Although one must realize the limitations of any single sampling method, the long-term and widespread use of bottom-set gill nets makes resultant data very useful for comparison with historical data in Pyramid Lake as well as for any between-lake comparisons.

The net used in this study encompassed a range of mesh sizes (1.27–8.89 cm bar mesh) to facilitate the capture of all species present. The selectivity curve indicates a representative sample of the adult size groups was

TABLE 2. Total species fish catch utilizing six different fishing methods in Pyramid Lake, Nevada.

Fishing gear	Habitat sampled	Time period	Number of samples	Number of fish	
				Cutthroat trout	Cui-ui
Bottom-set gill net	Inshore 0–15 m	11–75 to 12–75	153	636	289
	Offshore 46 m	11–75 to 12–77	152	496	11
	Pinnacles 0–15 m	2–76 to 12–77	23	86	40
	Delta 0–15 m	2–76 to 12–77	23	104	71
	Deep Benthic > 46 m	12–75 to 11–77	72	42	0
	Inshore (Below Thermocline) 23 m	6–77 to 11–77	35	270	10
Surface-set gill net	Inshore (Surface) 23 m	6–77 to 11–77	35	47	0
Vertical gill net	Limnetic (Vertical Water Column) 0–46 m	6–77 to 10–77	18	35	0
Fyke net	Inshore 0–15 m	12–75 to 12–77	147	46	2
Beach seine	Inshore 0–3 m	12n75 to 11–76	77	149	0
Otter trawl	Inshore 0–46 m	11–75 to 8–76	63	0	4
Total	ALL	11–75 to 12–77	798	1,911	427
Percent				2.61	0.58

*Mosquito fish were captured in small pools around the perimeter of the lake with a dip net.

achieved because the entirety of the curve for each species is contained within the 10 mesh sizes of the net (Fig. 2). The ascending right limb of each species-specific curve represents recruitment to the gear and indicates that juveniles were not adequately sampled by the gill net. The descending left limb is related to mortality, i.e., numbers decrease with increasing age and size. A 2.44 × 60.96 m gill net composed of four mesh sizes (10.16–17.78 cm bar measure) progressively larger than those of the standard net was

used to test how effective the standard net was in catching large cui-ui and trout. No large fish were captured with this net after 13 samples (only two small trout were caught by their teeth); this indicates that fish too large to be captured with the standard net were not abundant.

Percent species composition estimated from gill net catches compared to the other methods favored trout, cui-ui, and Tahoe sucker, and was least for tui chub. I believe the gill net samples underestimated the num-

Table 2 continued.

Fish species*							Total
Tahoe sucker	Tui chub	Sacramento perch	Lahontan redbside	Largemouth bass	Carp	Speckled dace	
2,960	14,996	72	0	0	1	0	18,954
675	6,671	0	0	0	0	0	7,853
775	1,834	19	0	0	0	0	2,754
695	1,618	17	0	0	4	0	2,509
18	1,567	0	0	0	0	0	1,627
631	1,975	3	0	0	0	0	2,889
2	2,657	1	0	0	0	0	2,707
0	5,227	0	0	0	0	0	5,262
373	23,608	61	0	0	1	0	24,091
29	3,514	1	26	0	1	1	3,721
82	711	8	0	1	1	2	809
6,240	64,378	182	26	1	8	3	73,176
8.53	87.98	0.25	0.04	TRACE	0.01	TRACE	100

ber of tui chubs due to the saturation effect observed when fish densities are high. Catch rates are depressed even by moderate catches, and it is possible to saturate nets to the point that they will catch no additional fish (Kennedy 1951). Spatial elimination of net area, visual stimulus, vibrations, and alarm substances (which chubs and suckers secrete) are some factors that cause saturation of gill nets (Meth 1970). Over 400 tui chubs have been captured in one 1.83×7.62 m mesh panel in Pyramid Lake during a one-day set. Cutthroat trout in Pyramid Lake are probably overestimated by gill net catches because they are frequently entangled by their jaws and teeth. As a result, trout (especially large ones) are vulnerable to almost all mesh sizes and are thus susceptible to much more netting area. This is indicated by the platykurtic catch curve for trout by mesh size.

Four Independent Sampling Methods

It is important to take into account the possible underestimation of tui chub in gill net data, especially when comparing the relative standing crops of cutthroat trout and tui chubs with respect to their predator-prey relationship. As independent comparisons, fyke net catches are composed of about 99 percent tui chubs, seine catches are composed of about 95 percent tui chubs, and trawls captured no trout.

The relative proportion of Tahoe sucker to trout is about the same, based on gill and trap net data. In contrast to the other fishing methods, the seine captured five times as many trout as Tahoe sucker. No adult trout

were captured in otter trawls and no cui-ui were captured in seines. The seine and trawl captured incidental species not taken by other methods.

To deal with the problem of fishing gear selectivity, the catch statistics of gill nets, fyke nets, seines, and otter trawls were used as independent estimates. By sampling during all seasons for a minimum of one year with each fishing gear, the species-specific variation in temporal availability is averaged out. Nevertheless, different amounts of fishing effort (net sets) were allocated to the various methods. Because I am assuming (for the sake of this relative abundance estimate) that each fishing method has equal validity, it is necessary to standardize fishing effort. I gave equal weight to each of the independent estimates by taking the mean of the C/f of the four sampling methods for each species, from which I calculated the percent species composition estimate. As can be seen in Table 3, inclusion of the three additional sampling methods shifts the relative abundance estimate in favor of the tui chub while not affecting the species rank. The proportions among the four less abundant species remain relatively constant.

Although the use of fyke nets, trawls, and seines compensated for the high density saturation of tui chubs in gill nets, other sampling problems existed. The various fishing methods were restricted with respect to lake zone sampled, therefore introducing spatial bias. For example, seines and fyke nets sampled only shallow water, and seines and otter trawls could only sample areas of relatively smooth substrate.

TABLE 3. Comparison of three relative abundance estimates of the five major fish species in Pyramid Lake, Nevada, 1976-1977.

Species	Percent species composition (bottom-set gill nets) (n = 373)	Percent of mean C/f of four sampling methods (gill and fyke nets, trawl, and seine) (n = 660)	Six habitat types weighted by proportion of lake volume (bottom, surface, and vertical gill nets) (n = 174)
Tui chub	77.92	91.43	97.27
Tahoe sucker	16.00	5.82	1.38
Cutthroat trout	4.07	1.86	1.29
Cui-ui	1.28	0.38	0.03
Sacramento perch	0.33	0.22	0.01

Six Habitat Types

The gill net sampling method was more flexible than other methods and with it I was able to sample various bottom depths and habitats within the two-year monthly sampling program. Percent species composition and catch rates in the various habitats varied substantially and verified the need for a spatially stratified design for the estimation of relative abundance. These gill net samples, however, were restricted to the benthic lake areas and did not adequately represent surface and limnetic waters. We overcame these problems by sampling a total of six ecotypes with three different types of gill nets.

Additional gill net sampling was conducted in surface inshore waters and the vertical limnetic water column. Thus, I obtained a stratified areal sample (utilizing various types of comparable variable mesh gill nets) that was representative of the most important habitats of Pyramid Lake (Table 4). The species composition and C/f in six ecotypes varied remarkably. Cui-ui, Tahoe sucker, and Sacramento perch were taken primarily in

shallow inshore areas. Previously discussed relative abundance estimates gave a disproportionate weight to these shallow littoral areas due to the sampling techniques employed. Realistically, however, shallow areas compose only a small proportion of the total lake area and volume. The relative proportions of the different ecotypes are presented in Figure 3. This diagrammatic separation of lake strata is admittedly arbitrary; however, considering the ecology of the fish species in Pyramid Lake and the areal differences in species diversity and relative species composition, I believe these strata represent discrete habitat types.

I calculated the third relative abundance estimate by weighting the C/f data of the six ecotypes with the proportion of the total volume of the lake each represents. Using this holistic perspective, the tui chub population composes over 97 percent of the total number of fish in Pyramid Lake. I believe this is the most realistic estimate of the relative abundance of each of the five major fish species in the Pyramid Lake fish population. Actually, tui chubs may be even more numerous

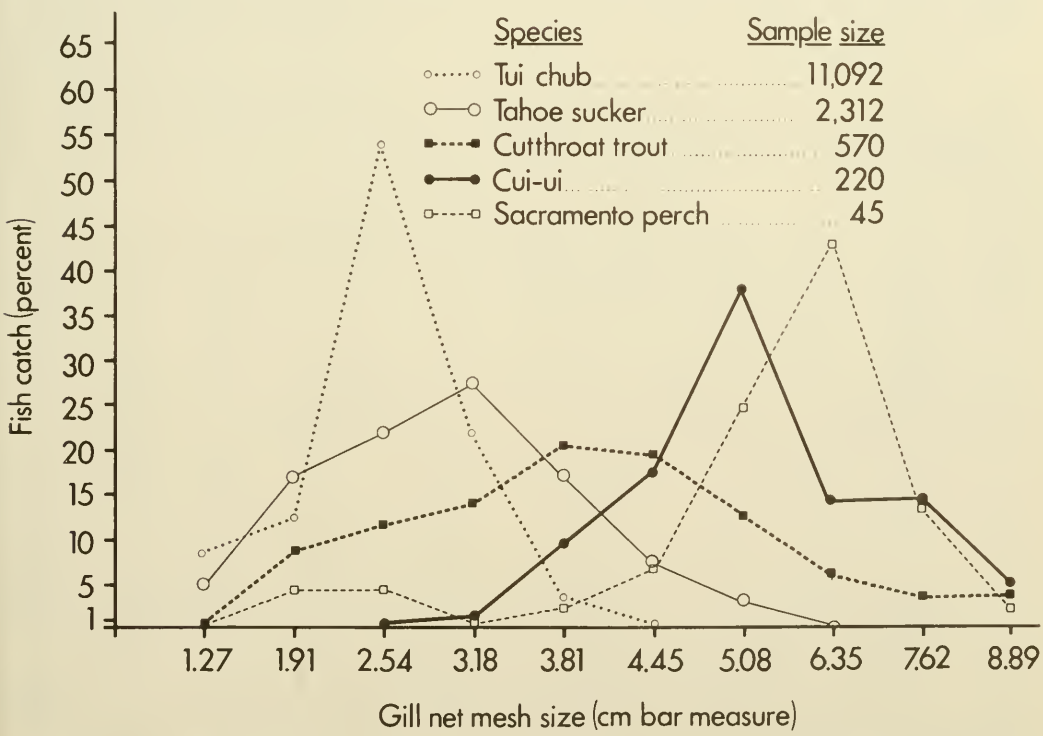


Fig. 2. Percent of the total species fish catch taken in 10 mesh sizes of variable mesh bottom-set gill nets in Pyramid Lake, Nevada, January–December 1976.

than this index indicates because gill nets in all ecotypes probably underestimate tui chubs and overestimate cutthroat trout.

Relative Biomass

The relative biomass of lacustrine fish populations is important for the evaluation of the bioenergetics of the ecosystem. Relative biomass is a function of the species specific weight and age composition as well as the numerical abundance of the population. Mean weight of a sample multiplied by the total catch of that species yields an estimate of the total relative weight of the catch, by species. Likewise, the product of the mean weight and the relative abundance estimate provides an index of the relative biomass of the population, assuming a representative sample (Table 5).

The relative species weight composition of the approximately 73,000 fish captured by all methods (Table 2) is naturally shifted toward the larger fish such as cutthroat trout (≈ 10.7 percent) and cui-ui (≈ 7.5 percent). Although the tui chub comprises the majority of the weight of the total catch (≈ 67 percent), this represents a much smaller proportion of the

catch than by numbers of individuals (≈ 88 percent). Nevertheless, as previously discussed, the total catch is not necessarily representative of the actual population, due to sampling bias. The index of relative numerical abundance presented in Table 4 is probably the most accurate basis for determining a relative biomass estimate. Thus, it is estimated that tui chubs compose about 90.4 percent of the biomass of the total fish population in Pyramid Lake and cutthroat trout compose about 6.4 percent. Theoretically, the biomass of a primary piscivore such as cutthroat trout may be as much as 20 percent of the biomass of fish forage (McConnell et al. 1978). Because cutthroat trout represent less than 7 percent of the combined biomass of tui chub and Tahoe sucker, there is apparently a substantial potential for increase in population size. In all cases the rank of species abundance remains constant.

Temporal Changes in Relative Abundance

Percent species composition and C/f data from our gill netting program were compared with similar gill net data collected by the Nevada Department of Fish and Game in

TABLE 4. Percent species composition and catch-per-unit effort of fish in six habitat types of Pyramid Lake from June through October 1977, and a numerical relative abundance estimate weighted by the volume of water in each habitat (derived from $C/f \times \text{volume}$):

Percent of total lake volume	Habitat	Depth zone	Bottom depth (m)	Number of samples	Fish species						TOTAL
					Catch statistic	Cutthroat trout	Cui-ui	Tahoe sucker	Tui chub	Sacramento perch	
1.27	Inshore littoral	Bottom	0-15	40	Percent	1.3	1.2	13.9	83.0	0.6	100
					Catch/net	2.8	2.4	29.1	173.0	1.3	208.6
9.30	Inshore below thermocline	Bottom	23	29	Percent	9.1	0.3	21.1	69.5	0.08	100
					Catch/net	7.8	0.3	18.1	59.7	0.07	86.0
10.65	Inshore above (0-4 m) thermocline	Surface	23	29	Percent	0.8	0	0	99.2	0.04	100
					Catch/net	0.7	0	0	88.4	0.03	89.1
8.46	Offshore	Bottom	46	30	Percent	10.8	0	11.0	78.2	0	100
					Catch/net	4.3	0	4.4	31.3	0	40.0
50.92	Offshore limnetic water column	Surface to 46 m	90	18	Percent	0.7	0	0	99.3	0	100
					Catch/net	1.9	0	0	290.4	0	292.3
19.40	Profundal	Bottom	61-100	28	Percent	3.0	0	0.19	96.8	0	100
					Catch/net	0.6	0	0.04	18.4	0	19.0
Numerical relative abundance (percent of: summed catch/net \times volume)						1.29	0.03	1.38	97.27	0.01	100

the 1950s (Table 6). Tui chubs and Tahoe suckers dominated the catches during both periods. Current cutthroat trout catches averaged much higher than 1954–1958, probably primarily due to stocking rates. Catches of Sacramento perch and carp were relatively low in both timme periods; however, current catch rates are substantially lower for both species. The most obvious change was the reduction of cui-ui C/f by half, and the decrease in its species composition from 4.4 percent in the 1950s to 1.3 percent presently.

Direct comparison of gill net catches from the two time periods was impossible, however, because the nets were not exactly the same. Also, most sampling in the 1950s was designed to capture target species in specific habitats, and the sampling during 1975–1977 was intended to be representative of all species in all lake areas throughout the year.

Two consecutive years (1976 and 1977) of data from our netting program, with identical fishing gear and a consistent temporal and spatial sampling design, provided a valid

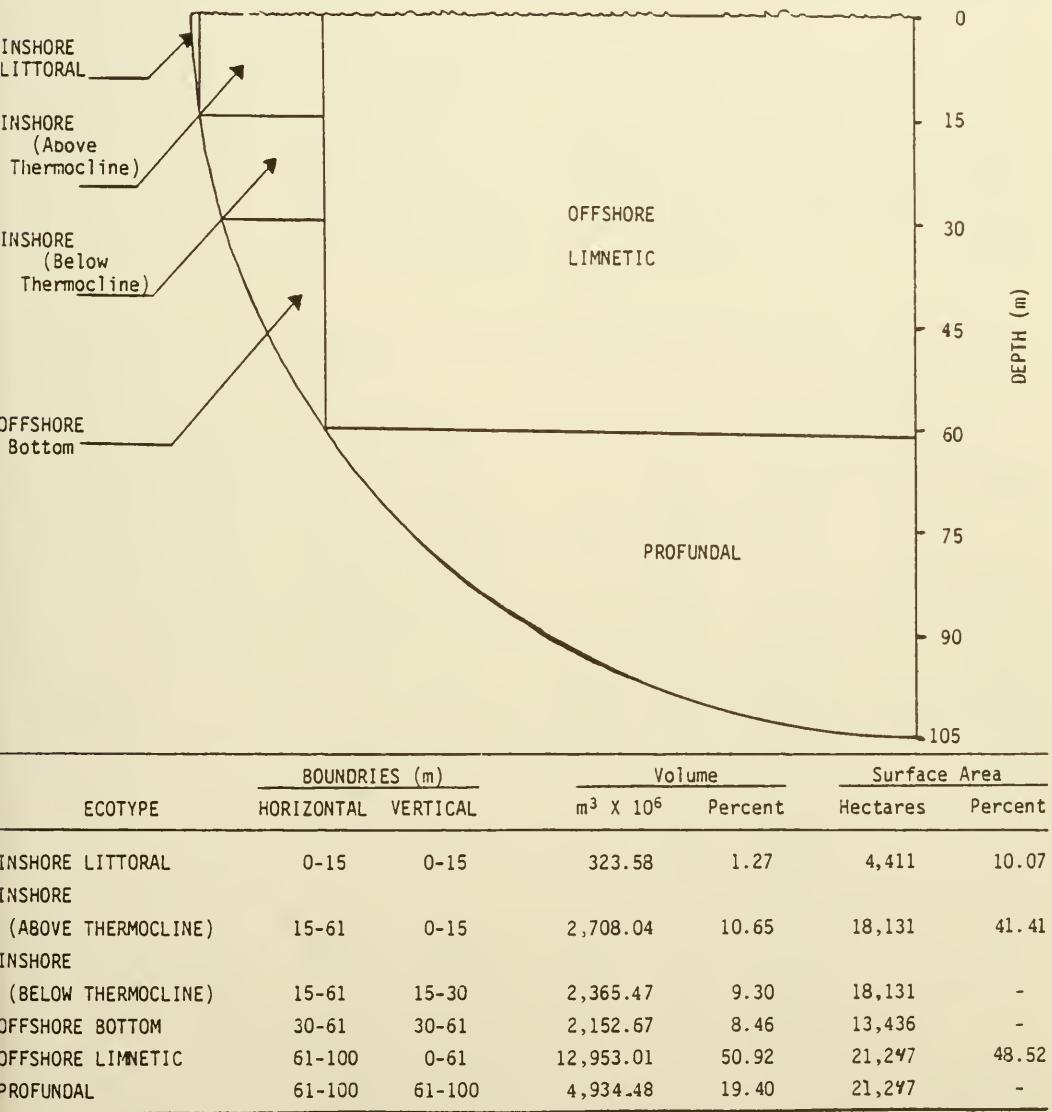


Fig. 3. Diagrammatic representation and relative proportions of stratified ecotypes of Pyramid Lake sampled during 1975–1977 (calculated for lake elevation 1155.2 m).

TABLE 5. Mean weight and relative biomass of fish in Pyramid Lake, Nevada.

Species	Sample weight (g)		Sample size (n)	Percent weight of total catch (derived from Table 2: percent of mean weight \times total catch)	Relative biomass (derived from Table 4: percent of mean weight \times numerical relative abundance)
	Mean	Maximum			
Cutthroat trout	481	5,450	676	10.68	6.41
Cui-ui	1,504	2,500	360	7.46	0.47
Tahoe sucker	186	1,480	286	13.49	2.65
Tui chub	90	830	322	67.34	90.42
Sacramento perch	485	1,200	104	1.03	0.05

documentation of current short-term trends. There was no statistically significant difference ($P>.05$) between 1976 and 1977 in the mean standardized (18-hour) gill net catch for any species (Table 7). The mean catch of Tahoe sucker and tui chub was almost identical during the two years, thus indicating stable populations. The mean catch of Sacramento perch was likewise close for the two years.

For cutthroat trout and cui-ui, the probability of a significant difference in annual means was about 80 percent. Although this probability level is not commonly considered statistically significant, I believe the changes in mean annual C/f for these species may reflect actual changes in fish abundance. The mean C/f of cutthroat was slightly higher in 1977 (3.4 versus 3.2 fish/net). This increase has probably resulted from progressively

TABLE 6. Catch data from 133 overnight gill net sets in Pyramid Lake during 1954–1958 (after Johnson 1958) compared to catch data from 373 overnight gill net sets in Pyramid Lake from November 1975 through December 1977.

Year	Number of net sets	Catch statistic	Kokanee	Trout*	Cui-ui	Tahoe sucker	Tui chub	Sacramento Carp	perch	Lahontan reidside	Total
1954–1955	45	Number	27	28	97	512	1,830	3	16	—	2,501
		Fish/net	0.60	0.62	2.16	11.38	40.67	0.07	0.36	—	55.58
		Percent	1.0	1.1	3.8	20.4	73.0	0.1	0.6	—	100
1955–1956	40	Number	48	29	104	498	1,968	3	45	—	2,695
		Fish/net	1.20	0.73	2.60	12.45	49.20	0.08	1.13	—	67.38
		Percent	1.7	1.1	3.8	18.4	73.0	0.1	1.6	—	100
1956–1957	21	Number	0	17	45	154	697	2	14	—	1,027
		Fish/net	0	0.81	2.14	7.33	33.19	0.10	0.67	—	48.91
		Percent	0	1.6	4.3	14.9	67.8	0.1	1.3	—	100
1957–1958	27	Number	2	7	61	247	1,033	3	6	—	1,359
		Fish/net	0.07	0.26	2.26	9.15	38.26	0.11	0.22	—	50.33
		Percent	0.1	0.5	4.4	18.1	76.0	0.2	0.4	—	100
1954–1958	133	Number	77	81	307	1,411	5,528	11	81	—	7,582
		Fish/net	0.58	0.61	2.31	10.61	41.56	0.08	0.61	—	57.01
		Percent	1.0	1.0	4.4	18.6	73.4	0.1	1.0	—	100
1976	177	Number	0	564	225	2,295	11,044	2	47	—	14,177
		Fish/net	0	3.19	1.27	12.97	62.40	0.007	0.27	—	80.10
		Percent	0	3.98	1.59	16.19	77.90	0.014	0.33	—	100
1977	172	Number	0	661	184	2,698	12,766	3	60	123	16,495
		Fish/net	0	3.84	1.07	15.69	74.22	0.017	0.35	0.69	95.90
		Percent	0	4.01	1.12	16.36	77.39	0.018	0.36	0.75	100
Nov. 1975–Dec. 1977	373	Number	0	1,325	415	5,205	23,345	5	108	123	35,526
		Fish/net	0	3.55	1.11	13.95	67.95	0.013	0.29	0.33	87.20
		Percent	0	4.07	1.28	16.00	77.92	0.015	0.33	0.038	100

*During 1954–1958, the "trout" category consists primarily of rainbow trout with a few cutthroat and brown trout. During 1975–1976, the "trout" category consists primarily of Lahontan cutthroat trout with a few cutthroat-rainbow hybrids.

TABLE 7. One-way analysis of variance to detect a significant difference between 1976 and 1977 mean standardized gill net catches of five fish species from Pyramid Lake. Data were transformed with $\log_{10}(y + 1)$.

Species	Mean catch (number/net)		F Statistic	Significance (P)
	1976 (n = 177)	1977 (n = 172)		
Cutthroat trout	3.20	3.40	2.02	0.156 ns
Cui-ui	1.29	0.95	1.58	0.210 ns
Tahoe sucker	13.98	13.98	0.45	0.504 ns
Tui chub	66.57	66.46	0.01	0.920 ns
Sacramento perch	0.29	0.33	0.09	0.766 ns

increasing stocking rates of hatchery fish during recent years. Of all species, only the cui-ui exhibited a decrease in C/f for the two-year period (from 1.29 to 0.95 fish/net). Although the within-year catches of this species are quite variable, the reduction in C/f may indicate that the lake's population decreased slightly from 1976 to 1977.

SUMMARY AND CONCLUSIONS

The fish population of Pyramid Lake is presently composed of the following species (in order of relative abundance): tui chub, Tahoe sucker, Lahontan cutthroat trout, cui-ui, Sacramento perch, Lahontan reddsides, carp, speckled dace, largemouth bass, and mosquitofish. The first five species comprise over 99.9 percent of the population; the others are of almost negligible importance to the ecosystem.

Tui chubs and Tahoe suckers, taken together, account for over 99 percent of the total fish population of Pyramid Lake by numbers and about 93 percent by weight. These cyprinids provide the primary forage base for the most important game fish in the lake—the Lahontan cutthroat trout.

Populations of tui chub, Tahoe sucker, and Sacramento perch are currently stable in Pyramid Lake. The Lahontan cutthroat trout may be increasing in abundance, probably due to hatchery stocking rates. The adult cui-ui population may be decreasing in abundance during 1976–1977, probably due to attrition of the older age classes, limited hatchery reproduction, and negligible natural reproduction.

Time, space, and fishing gear selectivity introduce variation that must be accounted for in relative fish abundance estimates. A sampling design stratified by the most important habitat types provides catch/effort data that can be weighted by the proportion of the total volume of the lake that each habitat represents; this approach provides the most reliable estimate of numerical relative fish abundance in lakes. It is important to consider the species specific size composition and relative biomass of the fish population, especially in terms of the bioenergetics of the ecosystem.

ACKNOWLEDGMENTS

The Pyramid Lake Paiute Tribe was instrumental in initiating the ecological research effort on Pyramid Lake. This study was funded under Bureau of Indian Affairs Contract H50C14209487. The entire Reno staff of W. F. Sigler and Associates, Inc., assisted with data collection.

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FEEDING INTERRELATIONS OF NATIVE FISHES IN A SONORAN DESERT STREAM

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ABSTRACT.— Native fishes in Aravaipa Creek, Arizona, cropped foods proportional to abundance of those foods within the system. Ephemeropteran nymphs and adults comprised the major prey of 5 of 7 fishes (*Gila robusta*, *Meda fulgida*, *Rhinichthys osculus*, *Tiaroga cobitis*, and *Catostomus insignis*). The omnivorous *Agosia chrysogaster* ate almost as many nymphal mayflies as did the carnivores. *Pantosteus clarki* was herbivorous, taking animals only when they were abundant. When ephemeropterans decreased in abundance, a shift by some fish species occurred to other locally or seasonally abundant items. Other fishes continued to feed upon the same foods throughout the year. Abundance of invertebrates in Aravaipa Creek, coupled with marked spatial partitioning of habitat by fishes present, seemingly precluded severe interspecific interactions for food.

This paper provides information on foods and feeding of native fishes in Aravaipa Creek, south-central Arizona. That low-desert stream is unique because seven native fishes still coexist under natural conditions, scarcely disturbed by foreign influences. Only one nonnative species, the green sunfish (*Lepomis cyanellus* Rafinesque), has succeeded in maintaining a small population within the system. Indigenous kinds include two catostomids, *Catostomus insignis* Baird and Girard (Sonora sucker) and *Pantosteus clarki* (Baird and Girard) (desert sucker), and five cyprinids, *Agosia chrysogaster* Girard (longfin dace), *Gila robusta* Baird and Girard (round-tail chub), *Meda fulgida* Girard (spikedace), *Rhinichthys osculus* Girard (speckled dace), and *Tiaroga cobitis* Girard (loach minnow). We examined stomachs for all but the round-tail chub, which was too rare during our study period to allow adequate sampling. Data on its foods, provided by James E. Burton, Arizona State University (ASU), were derived from specimens taken between 1965 and 1977 and housed in the ASU Collection of Fishes.

In addition to determination of how and what was eaten, we explored the question of food availability. Estimates of population densities and biomasses of potential and actual foods were made (Schreiber 1978), and those data were examined to determine how

selective, or how opportunistic, the fishes were in their feeding.

Some additional information has appeared on Aravaipa Creek fishes. Barber and Minckley (1966) published an account of the ichthyofauna, and later reported on foods of spikedace relative to season, ontogenetic changes, and habitat (Barber and Minckley 1981). Barber et al. (1970) presented additional data on biology of the spikedace, Minckley and Barber (1971) presented information from Aravaipa Creek in their general treatment of the biology of the longfin dace, and Minckley (1973, 1981) and Deacon and Minckley (1974) discussed several aspects of the ecology of the stream's fishes.

STUDY AREA

Aravaipa Creek in Graham and Pinal Counties, Arizona, originates in Desert Grassland between the Pinaleno and Galiuro mountains and flows northwest then west for more than 100 km. Much of the stream bed is dry, with permanent water surfacing at about 1010 m above mean sea level near the town of Klondyke. The stream then enters Aravaipa Canyon to flow between high, stony cliffs for about 20 km. Below the gorge the stream passes through Sonoran Desert in an ever-widening valley to disappear into its gravelly bed. In periods of high runoff, it

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enters the San Pedro River at about 660 m. More details on topography, geology, and ecology of the region were given by Ross (1925), Simons (1964), Bruns and Minckley (1980), and Minckley (1981).

The creek consists of riffles (15 cm deep and 1.5 to 4 m wide) separated by broad (8 to 15 m) reaches of shallow runs (<6 cm deep) flowing over sand and gravel through often-braided channels. Moving bedload precludes formation of pools typical of streams with more stable bottoms. Pool habitats in Aravaipa Creek (0.5 to 1.5 m deep) are present only where canyon walls or other obstacles restrict width of the channel or deflect currents to induce undercutting. Discharge of Aravaipa Creek near its lower end averages about 0.85 m³/sec, with a range of essentially 0.0 to 570 m³/sec (U.S. Geological Survey, published periodically). Drought persisted during our study period, and mean discharge from January 1975 through January 1976 was 0.33 m³/sec; range was 0.05 to 3.1 m³/sec.

METHODS AND MATERIALS

Selection of a sampling site was dictated by abundance of fishes and a consistent presence of the maximum number of species. The

selected reach consisted of a 60 m, rubble-bottomed riffle, bounded up- and downstream by broad, shallow runs with sand-gravel bottoms. Pool habitat was provided where the creek was deflected from a canyon wall (Fig. 1). Widths of the flowing channel and depths of various habitats changed with discharge, but closely resembled average conditions given above.

Field collections of fishes, benthos, and drifting materials were made over five 2-day periods in 1975–1976 (Table 1). Fishes were sampled by seines 9.5 m long, with 6.4-mm mesh (bar measure) and electrofishing gear of 110 volts, 1200 watts, alternating current. The number of fish preserved was limited to a maximum of 5–10 individuals per species every 4 hours to avoid depletion of local stocks over a 28-hour period. Fish sampling was done downstream from the drift and benthos site. Fishes were preserved intact in 10 percent formalin; no regurgitation upon preservation (Starrett 1950) was noted.

Only subadult and adult individuals of each species were studied. Stomachs, or the digestive tract anterior to the first loop toward the head in fish with poorly defined stomachs (Catostomidae), were excised and



Fig. 1. Photograph of the sampling area in Aravaipa Creek, Graham County, Arizona, summer 1975.

TABLE 1. Occurrence of potential and actual food items in samples of benthos, drift, and fish stomachs from Aravaipa Creek, Arizona, on five sampling dates in 1975-1976. Left to right, dates of collections were 9-10 January, 18-19 April, 11-12 July, 24-25 October (1975) and 30-31 January (1976). The symbol "x" denotes presence of the item on a given date, "-" indicates its absence, and the symbol "+" denotes occurrence of items in stomachs of *Gila robusta*, based on data provided by James E. Burton (see text).

Items	Benthos	Drift	Gila	Agosia	Meda	Rhin- ichthys	Tiaroga	Catos- tomus	Pant- osteus
COLLEMBOLA									
Undetermined taxa	-----	XXXXX	-	-----	-----	-----	-----	-----	-----
Sminthuridae	-----	X----	-	-----	-----	-----	-----	-----	-----
EPHEMEROPTERA									
Undetermined adults	-----	XXXXX	-	---XX	-X-XX	-----	-----	-----	-----
Baetidae nymphs	XXXXX	XXXXX	+	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX
Tricorythidae nymphs	XXXXX	XXXXX	+	XXXXX	XXXXX	-X-XX	--XXX	XXXXX	--X-
Heptageniidae nymphs	X--X	X--X	-	X--X	X----	X----	-----	X----	-----
Leptophlebiidae nymphs	XXXXX	XXXXX	+	XXXX-	XXXX-	-X---	-X---	-X---	-X---
Ephemerellidae nymphs	-X-X	-X---	-	-X---	-X---	-X---	-X---	-X---	-----
PLECOPTERA									
Capniidae adults	-----	X--X	-	X----	X----	-----	-----	X----	-----
Capniidae nymphs	X--XX	XX-XX	-	X--X	X--XX	X--X	X----	X-X-	X--X-
ODONATA									
Gomphidae nymphs	---XX	X-XX-	+	---X-	-----	-----	-----	X-XXX	-----
Libellulidae nymphs	---XX	-----	+	-----	-----	-----	-----	-----	-----
HEMIPTERA									
Undetermined terrestrial taxa	-----	XXXXX	-	-----	--XX-	-----	-----	-----	-----
Belostomatidae	-----	-----	+	-----	-----	-----	-----	-----	-----
Corixidae	---X	XXXXX	-	---X-	-X-	-----	-----	-----	-----
Mesoveliidae	-----	X-XXX	-	-----	-X---	-X---	-----	-----	-----
Microveliidae	-----	---X	-	---X-	-X---	-----	-----	-----	-----
Rhagoveliidae	---X-	-----	-	---X-	-----	-----	-----	-X-	-----
THYSANOPTERA									
Thripidae	-----	XXXX-	-	-----	-----	-----	-----	-----	-----
HOMOPTERA									
Undetermined taxa	-----	---X-	-	---XX	-XXXX	-----	-----	-----	-----
Aphididae	-----	XXXXX	-	-X---	--XX-	-----	-----	-----	-----
Cercopidae	-----	-----	-	---X-	--XX	-----	-----	-----	-----
TRICHOPTERA									
Undetermined adults	-----	--X-X	-	-----	--XXX	--X-X	--X-	-----	XX---
Helicopsychidae larvae	--X-	-----	-	-----	-----	-----	-----	-----	-----
Hydropsychidae larvae	X-XXX	-XXXX	+	-XXXX	--XXX	-XXXX	--XXX	XXXXX	----X
Glossosomatidae larvae	--XXX	--XXX	-	--XX-	--XX-	--XX-	-X-	-XXXX	--X-
Hydroptilidae larvae	X-X-X	-X---	+	-----	-----	-----	-----	-XXX-	-----
Limnophilidae larvae	-X-	-----	-	-----	-----	-----	-----	-----	-----
DIPTERA									
Chironomidae adults	-----	XXXXX	-	XXXXX	X-XXX	---X-	-----	X--X-	X----
Chironomidae larvae and pupae	XXXXX	XXXXX	+	XXXXX	-XXXX	XXXXX	XXXXX	XXXXX	XXXXX
Simuliidae adults	-----	XX-XX	-	--X-	-X-X-	-----	-----	-----	-----
Simuliidae larvae and pupae	XXXXX	XXXXX	+	XXX-X	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX
Tabanidae larvae	--X-	-----	-	-X-	-----	-----	--X-	--XX	-----
Ceratopogonidae larvae	XXX-	XXXX-	-	X----	X-X-	-XX-	-----	X-X-X	-----
Tipulidae adults	-----	-----	-	-----	-----	--X-	-----	-----	-----
Tipulidae larvae	-----	X----	-	X----	X-X-	-----	-----	--X-	-----
Dixidae larvae	---X	XX-X-	-	XX---	-X-	-X---	-----	-----	-----
Ephyridae larvae	X----	X--X	-	X----	X--XX	-----	-----	X--XX	-----
Muscidae larvae	---X-	-----	-	X----	-----	-----	-----	-----	-----
Stratiomyiidae larvae	-----	--X-X	-	-X-	-----	-X-	-----	--XX	-----
Empididae larvae	---X	X----	-	-----	-----	-----	X--X	-----	-----
Culicidae larvae	-----	X-X-	-	---X	-X-	-----	-----	--X-	-----

¹Na. = not applicable.

Table 1 continued.

Items	Benthos	Drift	<i>Gila</i>	<i>Agosia</i>	<i>Meda</i>	<i>Rhin- ichthys</i>	<i>Tiaroga</i>	<i>Catos- tomus</i>	<i>Pant- osteus</i>
LEPIDOPTERA									
Undetermined terrestrial adult	----	----	-	----	----	----	----	--X-	----
Pyralidae larvae	-X--	-X-X-		----	--X-	----	----	--X-	----
MEGALOPTERA									
Corydalidae larvae	----X	----	-	----	--X-	----	----	--X-	----
COLEOPTERA									
Undetermined terrestrial adults	----	XXXX-	-	--XX-	--XX-	----X	----	----	----
Curculionidae adults	----	----	-	----	----	----	----	--X-	----
Hydrophilidae adults	----	X-X--	+	----	----	----	----	----	----
Elmidae larvae	----X	X-XX-	-	----	----	----	----	--X-X	----
Dytiscidae larvae	----	X--X-	+	X--X	----	----	----	XX--	----
Staphylinidae adults	----	--XX-	-	----	--X-	----	----	----	----
Halipidae larvae	----	XX--	+	--X-	----	----	----	----	----
Dryopidae adults	----	----	+	----	----	----	----	----	----
HYMENOPTERA									
Undetermined terrestrial taxa	----	----	-	----	--X-	----	----	----	----
Ichneumonidae	----	----	+	----	----	----	----	----	----
Chalcidoidea	----	XXXX-	-	----	----	----	----	----	----
Formicidae	----	X-X--	+	----	--X-	----	----	----	----
MALLOPHAGA									
Undetermined terrestrial taxa	----	-XXX-	-	-X--	----	----	----	----	----
ACARINA									
Undetermined taxa	XXXXX	XXXXX	-	----	----	--X-	----	X-XXX	-X--
ARANEIDA									
Undetermined taxa	----	--X--	-	----	----	----	----	---X	----
CRUSTACEA									
Ostracoda (Cypridae)	--XXX	XXXXX	-	XXX-X	----	--X-	----	XXX-X	X----
Cladocera (Chydoridae)	----	-XX-X	-	----	----	----	----	---X	----
Copepoda (Cyclopoidea)	----	XXXXX	-	----	----	----	----	-X--	----
TARDIGRADA									
Undetermined terrestrial taxa	----	-X--	-	----	----	----	----	----	----
ANNELIDA									
Undetermined Oligochaeta	XX-XX	XXXXX	-	--X--	-X--	----	XX--	--X--	--X--
Undetermined Hirudinea	--X--	----	-	----	----	----	----	----	----
NEMATODA									
Undetermined taxa	X--X	XX--	-	XX--	--XX-	--X-	----	XXX-X	-XXXX
TURBELLARIA									
Planariidae	--X--	----	-	----	----	----	----	XXXXX	--X-X
HYDRAZOA									
Hydridae	---X	XXX-X	-	----	----	----	----	----	----
VERTEBRATA									
<i>Meda fulgida</i>	----	----	+	----	----	----	----	----	----
<i>Agosia chrysogaster</i>	----	----	+	----	----	----	----	----	----
<i>Sceloporus magister</i>	----	----	+	----	----	----	----	----	----
PLANT MATERIALS									
Diatoms	XXXXX	XXXXX	-	-XXXX	----	----	----	----	XXXXX
Filamentous algae	XXXXX	XXXXX	+	XXXXX	X----	X-X-	----	---X	--XXX
Detritus	XXXXX	XXXXX	+	XXXXX	--XX	--XX-	----	X--XX	---X-
INORGANIC MATERIALS									
Sand	Na. ¹	Na.	+	-XXX-	----	--XX-	----	---X	XXXXX

opened in the laboratory. The ingested animals were sorted to taxonomic categories in a gridded Petri dish. Other categories were inorganic materials (principally sand), finely divided organic material (detritus), filamentous algae, and diatoms. The volume of stomach occupied by each item was estimated visually using Hynes' (1950) point system. Each item in a stomach was assigned a value from greater than 0.0 to a maximum of 20.0, with the last indicating that 100 percent was represented by that item, and that the stomach was full. Each point, therefore, was equivalent to 5.0 percent of the total estimated stomach volume. Empty stomachs were scored 0.0 points and are included in compilations. Relative strengths and weaknesses of this technique were detailed by Hynes (1950) and Corbet (1961), who found estimation of relative volumes did not differ significantly from methods where quantities were measured directly. Actual volume of items or parts of items present were assigned points. No attempt was made to reconstruct live volumes of invertebrates from fragments (Ricker 1937).

Data for standing crops of benthic invertebrates were provided by Dale A. Bruns, ASU (Bruns 1977, Bruns and Minckley 1980). The drifting component of potential and actual food for fishes was collected by drift net and techniques described by Waters (1962). Sampling and analytic techniques, and tabular quantitative data on benthos and drift, are presented by Schreiber (1978) and are discussed here only in general terms relative to feeding of fishes.

Marked diel periodicity of drift of aquatic invertebrates (Waters 1962, 1972), and of feeding of fishes (Ivlev 1961), were compensated for by computing means for each over the 28-hour sampling periods. Standing crops of benthos were estimated by the mean of two samples per period. Compilation of data was performed on a Univac 1110/42 computing system (Arizona State University Computing Center).

RESULTS

Foods Available to Fishes

A total of 75 potential or actual food items was taken in samples of benthos, drift, and fish stomachs from Aravaipa Creek (Table 1). Of these, 69 (93.3 percent) were invertebrates. Vertebrates (three species) were eaten only by roundtail chub, and species diversity of plant materials was not assessed. Inorganic material (sand) was excluded from the gross number of items, but was common in stomachs of *Pantosteus clarki* and occasionally in *Agosia chrysogaster*, *Rhinichthys osculus*, and *Catostomus insignis*.

Of invertebrate taxa, 36 kinds (52.2 percent) were nymphs, pupae, or nonemerging adults of aquatic insects. Noninsect aquatic animals made up 13 percent (9 groups), emergent adults of aquatic groups, 8.8 percent (6 groups), and 26.1 percent (18 taxa) were of terrestrial origin.

Only a few invertebrate taxa were consistently present in both benthos and drift samples (Table 1). Genera of the family Baetidae (*Baetis*, *Callibaetis*, and *Centroptilium*) comprised most of the mayfly biomass, and they were also highest in numbers. Tricorythidae (*Tricorythodes*) and Leptophlebiidae (*Choroterpes* and *Leptohypes*) were far less abundant than Baetidae, but were equally as frequent in occurrence. Heptageniidae (*Rithrogena*) and Ephemerellidae (*Ephemerella*) nymphs were seasonally abundant (winter-spring) in benthic samples and were present in drift during the same periods.

Larvae and pupae of the dipteran families Chironomidae and Simuliidae were present in all periods, both in drift and benthic samples. They were relatively important in terms of biomass, and were often present in large numbers. Adult chironomids were present in all drift samples, forming significant proportions of the biomass. Adult simuliids were uncommon in drift, but were taken in 4 of 5 sampling periods.

Water mites (Acarina) and microcrustaceans, especially cyprid ostracods, also were relatively consistent in occurrence in benthic and drift samples, but were of minor consequence in biomass.

Trichopteran larvae of the genera *Hydropsyche* and *Cheumatopsyche* (Hydropsychidae) were scarce early in the study, but became important later as major components of biomass in benthic samples and as relatively common taxa in drift. Glossosomatidae trichopterans followed a similar trend. High biomass estimates for trichopterans, especially Hydropsychidae, typically resulted from a few large individuals rather than from dense populations.

A large number of other animals were in benthic and drift samples (Table 1), some in small numbers or only occasionally, and others seasonally. Especially seasonal in abundance was the Capniidae plecopteran, *Mesocapnia frisoni*, occurring only during cool weather, and turbellarians in the benthos in summer.

Interrelations of Benthos and Drift

Variance in samples from benthic communities is notoriously high (Elliott 1971), presumably as a result of heterogeneity of stream habitats joined with diversified life histories and behaviors of faunal constituents. Drift of certain organisms (*i.e.*, Baetidae) has, however, been demonstrated as consistent and predictable, and has been proposed as a measure of invertebrate populations in streams that may be more sensitive than direct sampling of benthos (Waters 1965, 1972). Mixing action of turbulence tends to suppress effects of heterogeneity.

The relationship between drift and standing crop of benthos at a given place is only a general one, especially if habitats upstream vary significantly from that at the point of sampling. Waters (1965) estimated on the basis of blocking a stream that organisms drifting at a given place originated no more than 50 or 60 m upstream. Our comparisons of standing crops of benthos and drift were justified by similarity of habitat throughout the reach and by lack of statistical differences in numbers and biomass at our station and another site immediately above (Bruns 1977). Samples of drift and benthos were always taken midway in a 60-m-long, uniform riffle, so comparative integrity of data was maintained.

A total of 36 items occurred in samples of benthos: 26 (72.2 percent) were nymphs, larvae, pupae, and nonemerging adults of aquatic insects, 7 (19.4 percent) were other aquatic invertebrates, and 3 (8.3 percent) were nonanimal categories (algae, diatoms, and detritus). Drift sampling caught items of 66 taxa. Of these, 27 (49.1 percent) were aquatic insects, 5 (9.1 percent) were emergent adults of aquatic insects, 7 (12.7 percent) were other aquatic invertebrates, and 13 (23.6 percent) were invertebrates of terrestrial origin. Three (5.5 percent) were the nonanimal components defined above.

Invertebrates common to drift and benthos included all important categories discussed before (Table 1). Slightly more than 65 percent of drift (excluding nonanimal components) was derived from benthos, and this rose to 75 percent when emerged adults of aquatic insects were included. Three of four items in drift of Aravaipa Creek were, therefore, autochthonous to the system. Of 32 benthic taxa recorded (again excluding nonanimal items), 23 (71.4 percent) drifted. Groups of benthic animals absent from drift included Libellulidae (dragonflies), Tabanidae (horseflies), Muscidae (muscid flies), Rhagoveliidae (water striders), Helicopsychidae and Limniphilidae (caddisflies), Corydalidae (hellgrammites), Hirudinae (leeches), and Turbellaria (flatworms). Absence of all but the last from drift may be generally attributed to their rarity. Turbellarians appeared to resist drifting. Of organisms drifting, only baetids and *Tricorythodes* mayflies and chironomid dipteran larvae and pupae were present in all samples on all sampling dates.

Foods of Fishes

Nymphal mayflies comprised 57 percent or more of stomach contents of 5 of 6 fish species analyzed quantitatively (Fig. 2). Only the herbivorous *Pantosteus clarki* contained few ephemeropterans. Dipteran larvae were most common in stomachs of bottom-dwelling fishes, *Rhinichthys osculus*, *Tiaroga cobitis*, and *Catostomus insignis*. Trichopteran larvae were less than 10 percent of total food volumes in all but *T. cobitis*, but present in significant amounts in all but *P. clarki* stomachs.

Plecopteran nymphs were also eaten in small amounts by all species, but *P. clarki* contained only traces of that taxon (Fig. 2). Turbellaria were heavily preyed upon by *C. insignis* and *P. clarki* when present in summer, but not by other fishes. Winged insects (including both emerged aquatic forms and scarcer terrestrial kinds) were consumed in more than trace amounts by *Meda fulgida*, *Agosia chrysogaster*, and *R. osculus* in decreasing order of volumes. Other than *P. clarki*, only *A. chrysogaster* consumed substantial amounts of vegetative material. Animals eaten in volumes too low for visual quantification in Figure 2 are listed in Table 1. When all potential foods are considered, 66 (88 percent) of the 75 items were found in at least one species of fish.

Accounts of Species

ROUNDTAIL CHUB.— Chubs (*Gila robusta*) ate 21 items, including many principal foods of other species (Table 1). The diet strongly reflected its large body size (to 38.5 cm total length in Aravaipa Creek), expansive, terminal mouth, and raptorial pharyngeal teeth. Many food items were large in size, and mastication was apparent (Burton, pers. comm.). Chubs are secretive animals, inhabiting deeper water near cover; yet occurrence of terres-

trial organisms such as an iguanid lizard and ants, and a variety of benthic inhabitants (e.g., Odonata naiads), other fishes, and Belostomatidae hemipterans, indicates active feeding from bottom to surface. Uniqueness of this diet was exemplified by only 38.1 percent of the food items also being consumed by other fish species. Six (28.6 percent) items found in *Gila robusta* stomachs did not appear in other fishes.

LONGFIN DACE.— Thirty-nine kinds of foods were tallied from stomachs of *Agosia chrysogaster*, and algae made up a substantial proportion of the diet (Table 2, Fig. 3). *Cladophora glomerata*, the dominant filamentous alga in the channel (Bruns and Minckley 1980), was rarely present. Diatoms and unattached green algae (*Mougeotia* sp. and *Spirogyra* sp.) were abundant in stomachs, and blue-green filamentous forms such as *Oscillatoria* sp. occasionally were present. These organisms are characteristic of stream margins and quiet areas near beds of higher plants, and their presence reflected grazing by longfin dace in such places.

Fisher et al. (1981) considered longfin dace to be herbivorous in Sycamore Creek, Arizona, but large volumes of invertebrates were in stomachs from Aravaipa Creek. Of ephemeropteran nymphs eaten by longfin dace, the ubiquitous baetids predominated in 4 of 5

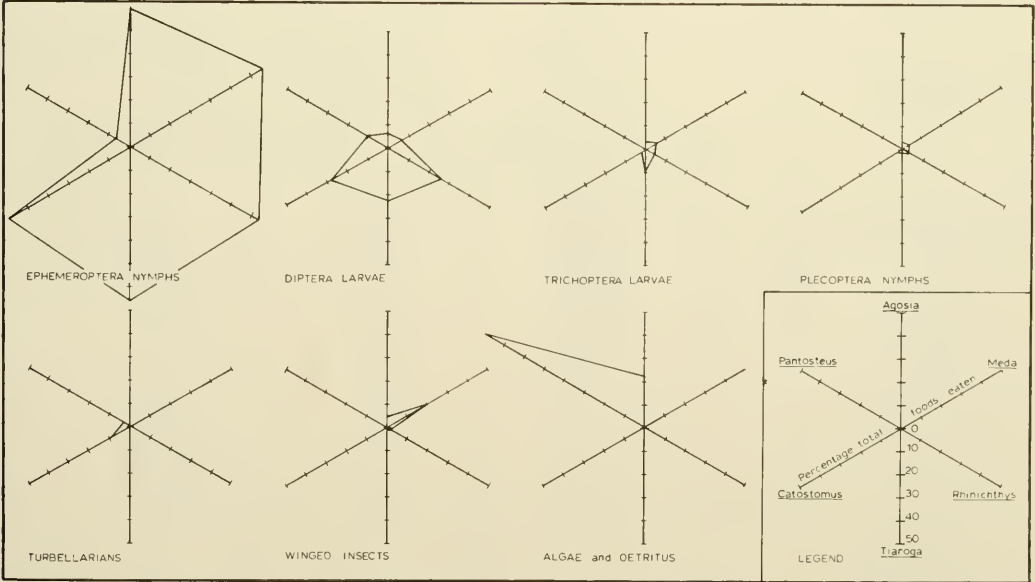


Fig. 2. Annual averages of relative percentages of major food items eaten by six species of fishes in Aravaipa Creek, Arizona, 1975-1976.

sampling periods (ranging from 23 to 61.4 percent of total foods). Relationship between drift biomass of baetids and occurrence in longfin dace stomachs seemed strong ($r = 0.81$). There was no obvious relationship between benthic standing crop and stomach contents ($r = <0.5$). *Tricorythodes* mayflies were preyed upon in all but the January 1975 period, occupied more volume in April than did baetids (36.5 percent vs. 24.2 percent), and were eaten in substantially smaller amounts than baetids in the periods July 1975 through January 1976. *Tricorythodes* spp. rarely achieved half the numbers or biomass of baetids in drift or benthos (Schreiber 1978); thus some special association with longfin dace was indicated. The three species recorded by Bruns (1977) from Aravaipa Creek, *T. condylus*, *T. dimorphus*, and *T. minutus*, were most abundant in sand-bottomed areas. Longfin dace shared this tendency to be most abundant in open, sandy areas, with moderate current, in water <10 cm deep (especially in periods of lower light intensity; Minckley and Barber 1971).

Leptophlebiidae and *Rhithrogena* sp. mayflies made up only a small proportion of the diet of longfin dace. The former were present as 14 percent of total food volume in July and were absent or in trace amounts in other months (Table 3), despite their consistent presence in both benthos and drift (Table 1).

The common leptophlebiids (*Choroterpes inornatus*) and *Rithrogena* sp. are both rheophilic and associated with cobble-bottomed rapids in Aravaipa Creek (Bruns 1977), a habitat rarely occupied by longfin dace. *Rhithrogena* sp. was, however, present in stomachs of *A. chrysogaster* in their period of occurrence (January of both years).

Plecopteran nymphs were eaten during their winter occurrence. Appearance of Hydropsychidae larvae (Trichoptera) in stomachs corresponded well with a spectacular increase in their biomass in benthos in January 1976—and with an increase in drift during that period, although far less impressive (Schreiber 1978). The increase in volumes eaten resulted from a few large individuals, rather than from increases in numbers, as also occurred in benthos samples.

Dipteran larvae made up a substantial percentage of total food in *A. chrysogaster* only in January 1975, the same period during which chironomid and simuliid larvae were most common in drift. A gradual decline in drift of dipterans throughout the study was paralleled by a continuing drop in volumes in the diet. Occurrences of Chironomidae and Simuliidae in benthic samples were consistent, but variations in standing crops did not correspond to those in stomachs. Chironomids are a diverse group, generally distributed within the stream. The small

TABLE 2. Food habits of longfin dace, *Agosia chrysogaster*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parenthesis.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (70)	Apr (32)	Jul (40)	Oct (40)	Jan (41)	Jan	Apr	Jul	Oct	Jan
Ephemeroptera nymphs	9.7	17.8	4.7	6.2	24.9	45.1	60.7	47.0	68.9	66.8
Baetidae	8.6	7.1	2.3	3.9	22.9	40.0	24.2	23.0	43.3	61.4
Tricorythidae	—	10.7	1.0	2.3	2.0	—	36.5	10.0	25.6	5.4
Leptophlebiidae	Tr.	—	1.4	Tr.	—	Tr.	—	14.0	Tr.	—
Heptageniidae	1.1	—	—	—	Tr.	5.1	—	—	—	Tr.
Plecoptera nymphs (Capniidae)	2.2	—	—	—	1.1	10.2	—	—	—	3.0
Trichoptera larvae (Hydropsychidae)	—	Tr.	Tr.	Tr.	3.5	—	Tr.	Tr.	Tr.	9.4
Diptera larvae, pupae	6.1	1.3	Tr.	Tr.	Tr.	28.4	4.4	Tr.	Tr.	Tr.
Chironomidae	3.7	Tr.	Tr.	Tr.	Tr.	17.3	Tr.	Tr.	Tr.	Tr.
Simuliidae	2.4	1.3	Tr.	Tr.	Tr.	11.2	4.4	Tr.	Tr.	Tr.
Winged insects	1.4	3.7	Tr.	Tr.	6.5	12.6	Tr.	Tr.	Tr.	Tr.
Ephemeroptera	—	3.7	—	Tr.	Tr.	6.5	12.6	Tr.	Tr.	Tr.
Chironomidae	1.4	Tr.	Tr.	Tr.	Tr.	6.5	Tr.	Tr.	Tr.	Tr.
Algae (Filamentous algae)	2.1	6.5	5.3	2.8	7.8	9.8	22.2	53.0	31.1	20.8

occurrence of rheophilic simuliids, however, tends to substantiate a lack of feeding by longfin dace on turbulent riffles.

Winged insects in stomachs of longfin dace, especially trace amounts of terrestrial coleopterans and homopterans (Table 1), indicated some feeding at the surface. Nevertheless, correspondence of frequencies of adult ephemeropterans and chironomids in drift and in stomachs was far less than perfect. Both taxa drifted throughout the year,

and chironomids were consistently taken by *A. chrysogaster* and mayflies were not. Perhaps the relatively larger size of some adult mayflies caused the small-mouthed longfin dace to select against them. The dace ate more mayfly adults in April, although they drifted most abundantly in January of both years, and more chironomid adults were eaten in January 1975 than in January 1976, when they were equally abundant in drift.

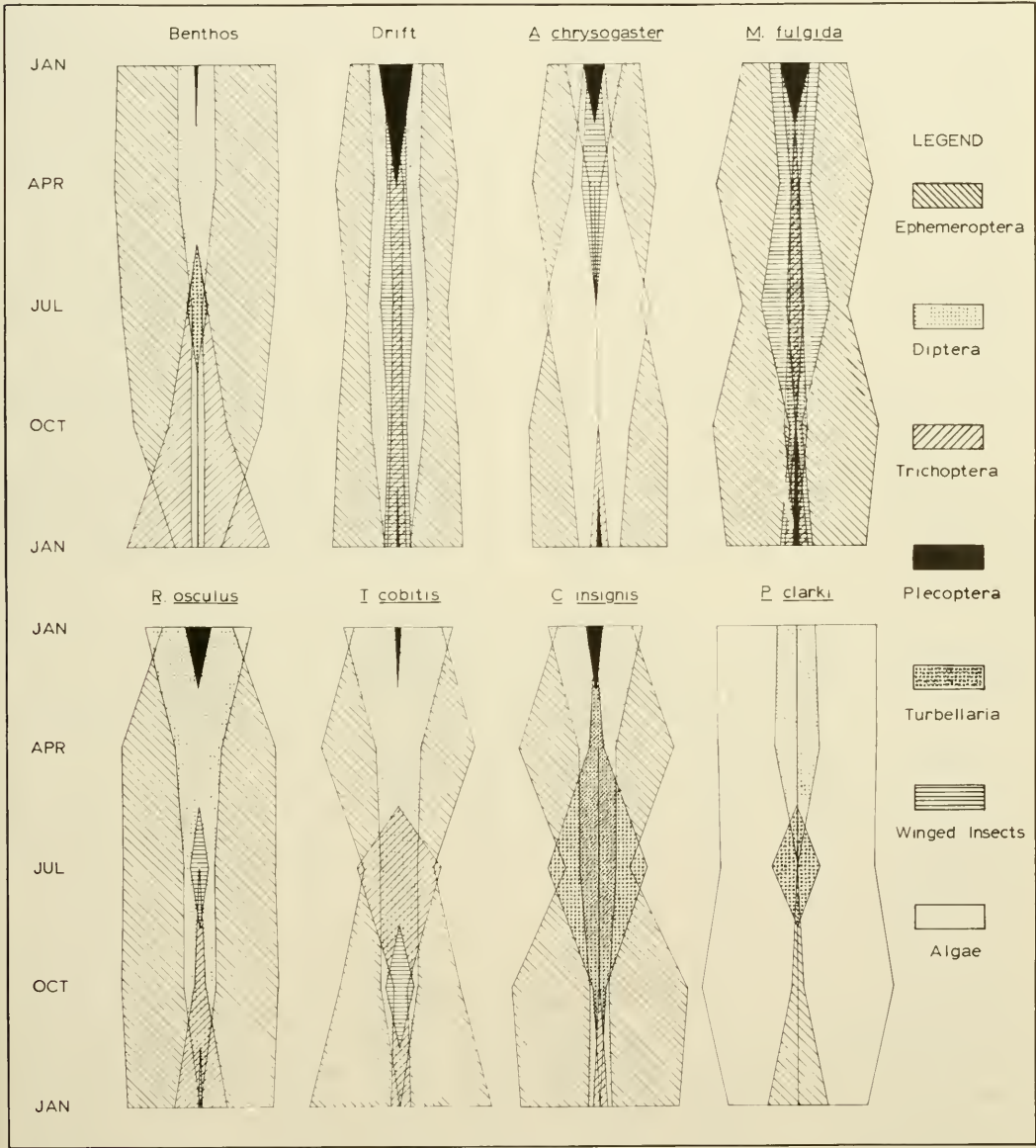


Fig. 3. Relative abundance (by weight) of major invertebrate taxa in benthos and drift, and of invertebrate taxa and algae in stomachs (by volume) of fishes from Aravaipa Creek, Arizona, 1975–1976.

SPIKEDACE.— Patterns of use of nymphal ephemeropterans by *Meda fulgida* in Aravaipa Creek closely followed those just described for *Agosia chrysogaster* (Table 3). Spikedace occupy pools, or areas of deeper water below riffles (Miller and Hubbs 1960). In Aravaipa Creek, where pools are essentially absent, it is typically found in middle to surface depths of deeper parts of the channel, or in riffles and runs of moderately swift current. Spikedace are relatively small (<75 mm total length), highly mobile fish, moving continuously and visually inspecting drifting materials at the surface and within the water column. Gustatory inspection also is commonly practiced, items being taken into the large, terminal mouth, moved about, then swallowed or rejected. The 36 food items recovered from stomachs illustrates its versatility. A high percentage (22 percent) of terrestrial organisms, few of which were eaten by other species (Table 1), produced a diet qualitatively as unique as that of *Gila robusta*.

Total volumes of Baetidae in stomachs and biomass of drift did not correlate as highly for *M. fulgida* ($r = 0.68$) as it did for *A. chrysogaster*. Baetids in benthos were not related to total volumes in spikedace stomachs ($r = <0.5$). *Tricorythodes* spp. nymphs in benthos were correlated with total volumes

in spikedace ($r = 0.91$), but no such relationship was apparent between stomach volumes and drift ($r = <0.5$). Again, sandy bottomed areas of the channel occupied by both *Tricorythodes* spp. nymphs and spikedace presumably enhanced their interrelationship. Leptophlebiids, *Rhithrogena* sp., and *Ephemerella* sp. nymphs made up only minor parts of the diet. The first of these did, however, contribute 13 percent in a single sampling period (July).

Plecoptera nymphs were used by spikedace when present, most frequently in January 1978, when they were also most common in drift (Fig. 3). Hydropsychid larvae (Trichoptera) were in stomachs in all but the first sampling period and were major contributors to total food volume in July 1975 and January 1976. These organisms made up a disproportionate percentage in July (8 percent) as compared to their low relative abundance in benthos and drift (2.7 and 1.5 percent, respectively), perhaps indicating selection by the fish.

Spikedace fed more heavily upon winged insects than did any other fish species in Aravaipa Creek, with an average total volume throughout the study of more than 20 percent (Figs. 2–3). Mayfly adults were generally most abundant, paralleled or closely followed by chironomid adults. Opportunism seemed

TABLE 3. Food habits of spikedace, *Meda fulgida*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parentheses.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (28)	Apr (22)	Jul (33)	Oct (37)	Jan (20)	Jan	Apr	Jul	Oct	Jan
EPHEMEROPTERA NYMPHS	28.2	50.7	19.2	20.4	41.8	52.2	78.0	53.0	83.0	69.6
Baetidae	24.4	36.6	9.6	17.7	40.5	45.3	56.3	26.5	72.0	67.5
Tricorythidae	2.0	12.4	4.9	2.7	1.3	3.6	19.1	13.5	11.0	2.1
Heptageniidae	1.8	—	—	—	—	3.3	—	—	—	—
Leptophlebiidae	Tr.	Tr.	4.7	Tr.	—	Tr.	Tr.	13.0	Tr.	—
Ephemerellidae	—	1.7	—	—	—	—	2.6	—	—	—
PLECOPTERA NYMPHS (Capniidae)	7.0	—	—	Tr.	1.5	12.9	—	—	Tr.	2.5
TRICHOPTERA LARVAE (Hydropsychidae)	—	1.7	2.9	Tr.	7.3	—	2.6	8.0	Tr.	12.1
DIPTERA LARVAE, PUPAE	7.4	2.8	2.0	2.8	Tr.	13.8	4.4	5.5	11.5	Tr.
Chironomidae	5.0	1.4	2.0	Tr.	Tr.	9.3	2.2	5.5	Tr.	Tr.
Simuliidae	2.4	1.4	Tr.	2.8	Tr.	4.5	2.2	Tr.	11.5	Tr.
WINGED INSECTS	11.2	9.8	12.1	1.4	9.5	20.5	15.1	33.5	5.5	15.8
Ephemeroptera	7.0	9.8	Tr.	1.4	6.0	12.9	15.1	Tr.	5.5	10.0
Chironomidae	4.2	Tr.	1.5	Tr.	Tr.	7.6	Tr.	4.2	Tr.	Tr.
Trichoptera	—	—	10.6	Tr.	3.5	—	—	29.3	Tr.	5.8

the rule in *M. fulgida*, and active feeding on emerging trichopterans was apparent in July. Trichopteran adults made up 29.3 percent of total volume of the diet in that sampling period (Table 3).

SPECKLED DACE.— This dace has a strong proclivity for riffles within a broader range of habitat selection (Minckley 1973). Its diet in Aravaipa Creek, which consisted largely of rheophilic insects (Table 4), reflected this habitat preference. Food habits of *Rhinichthys osculus* overlapped widely with those of *Agosia chrysogaster* and *Meda fulgida*, however, with more than 80 percent of its foods also eaten by the other two fishes.

Ephemeropteran nymphs made up more than 70 percent of total food volume in *R. osculus* in all but the first sampling period (Figs. 2–3). *Tricorythodes* and leptophlebiid nymphs, species of sand-bottomed channels and cobble-bottomed rapids, respectively, had a combined volume exceeding that of baetids in April and July (Table 4). This resembled the pattern for *A. chrysogaster* in the same periods (Table 2), but was distinct from that for *M. fulgida* (Table 3), where baetids dominated stomach contents.

Plecopteran nymphs were preyed upon when present in winter, and in greatest quantities in winter 1975. Hydropsychid larvae (Trichoptera) increased in importance from July 1975 to become a major component of

total foods consumed in January 1976, following the increase in caddisflies in both benthos and drift.

Dipteran larvae and pupae were more heavily used by the bottom-feeding speckled dace than by either longfin dace or spike-dace. High initial levels of predation by *R. osculus* on dipterans gradually declined, however, parallel to indicated availability; simuliids were heavily used, further documenting foraging by speckled dace in riffles.

Trichopteran adults were taken by *R. osculus* in July and January 1976. Because speckled dace rarely move near the surface, it is likely adult caddisflies were caught during emergence from benthic puparia. Only one of 23 food items recorded for speckled dace was of terrestrial origin (Table 1), further supporting the rarity of surface feeding by this minnow.

LOACH MINNOW.— This species was rare in Aravaipa Creek during the period. A total of 47 individuals was examined, with a range per sampling period of 3 to 14 individuals (Table 5). This diminutive minnow is current loving and benthic in habit, living exclusively on riffles <15 cm deep (Minckley 1965, 1973).

This restriction in habitat was manifested in an equally limited diet (Figs. 2–3). Only 11 items were tallied from stomachs of *Tiaroga cobitis*, and only 2 are sometimes associated

TABLE 4. Food habits of speckled dace, *Rhinichthys osculus*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parenthesis.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (12)	Apr (6)	Jul (38)	Oct (36)	Jan (34)	Jan	Apr	Jul	Oct	Jan
Ephemeroptera nymphs	17.1	27.5	23.3	17.7	16.8	34.7	76.8	76.2	79.0	72.9
Baetidae	15.0	8.3	10.3	16.5	16.8	30.5	23.3	33.6	73.3	71.1
Tricorythidae	—	10.0	5.8	1.2	Tr.	—	27.9	18.9	5.3	1.8
Heptageniidae	2.1	—	—	—	Tr.	4.2	—	—	—	Tr.
Leptophlebiidae	—	6.7	7.2	—	—	—	18.6	23.7	—	—
Ephemerellidae	—	2.5	—	—	—	—	7.0	—	—	—
Plecoptera nymphs (Capniidae)	6.3	—	—	—	Tr.	12.7	—	—	—	Tr.
Trichoptera larvae (Hydropsychidae)	—	—	Tr.	1.0	6.2	—	—	Tr.	4.6	26.1
Diptera larvae, pupae	25.8	8.3	4.7	3.7	Tr.	52.6	23.3	15.0	16.3	Tr.
Chironomidae	5.8	5.8	1.9	1.8	Tr.	11.9	16.3	7.0	7.9	Tr.
Simuliidae	20.0	2.5	2.8	1.9	Tr.	40.7	7.0	9.0	8.5	Tr.
Winged insects (Trichoptera)	—	—	2.6	—	Tr.	—	—	8.6	—	1.1

with nonriffle habitats (*Tricorythodes* spp. nymphs and Tabanidae dipteran larvae, the latter occurring only as a trace; Table 1). Ubiquity of baetid nymphs and chironomid larvae reduce their value in interpretation of feeding habitats of the minnow, but both are common on riffles. Cobble-inhabiting, swift-water forms such as *Rhithrogena* sp. and leptophlebiid nymphs reflect occupation of riffles by the fish, as do the large percentage of simuliids eaten early in the study (Table 5). Of other fishes in the stream, only *Gila robusta* used less than 80 percent of the same food items depended upon by *T. cobitis*, and most species ate more than 90 percent.

Ephemeropteran nymphs made up most of the diet of *T. cobitis* during three sampling periods. Baetids were most important in each instance. *Tricorythodes* spp. nymphs were abundant in stomachs only in April, leptophlebiids were similarly abundant in July 1975 and January 1976, and *Ephemerella* sp. were eaten in moderate quantities when abundant in April (Table 5). Active selection for trichopteran larvae by loach minnows was indicated in July. Neither family of caddisfly larvae that were consumed were abundant in drift or benthos at that time; yet hydropsychids made up 28.2 percent of total food volume, and glossosomatids 18.8 percent. Neither group was in stomachs in January and April 1975 (perhaps because of small sample size in April), and only hydropsychids persisted in October 1975 and January 1976.

The gradual decline in percentages of dipteran larvae in stomachs of other minnow species throughout the study was less pronounced in *T. cobitis* because of its cropping of simuliids in all but the last sampling period. Chironomid larvae were a minor component of diet of the loach minnow (Table 5).

Winged trichopterans appeared in stomachs in October, presumably being captured upon emergence from puparia. Loach minnows cannot maintain position in midwater without violent swimming, due in part to a greatly reduced air bladder. Feeding from the surface or even midwater in areas of turbulence is therefore unlikely. It is interesting, however, that regression coefficients between stomach volumes of *T. cobitis* and some components of drift were relatively high (e.g., for total ephemeropterans, $r = 0.86$), and no such relationships were apparent between benthic biomass and stomach contents. The fish may directly sample areas from which drift is derived, and the gross estimation of benthic communities afforded by our sampling was far less adequate.

SONORA SUCKER.— This large species exhibited a generalized, carnivorous diet in Aravaipa Creek. The fish is typically a pool dweller (Minckley 1973), living on the bottom in areas near undercut banks, boulders, or logs and other debris. It will sometimes visit midwater and, despite the ventral mouth, has been observed taking foods there. Although the diet of *Catostomus insignis* was

TABLE 5. Food habits of loach minnow, *Tiaroga cobitis*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parentheses.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (12)	Apr (3)	Jul (14)	Oct (12)	Jan (6)	Jan	Apr	Jul	Oct	Jan
EPHEMEROPTERA NYMPHS	30.0	35.0	9.8	16.5	55.8	43.7	77.7	34.6	61.6	90.6
Baetidae	30.0	25.0	7.5	16.5	47.5	43.7	55.6	26.5	61.6	77.1
Tricorythidae	—	7.5	Tr.	Tr.	2.5	—	16.7	Tr.	Tr.	4.1
Leptophlebiidae	Tr.	—	2.3	Tr.	5.8	Tr.	—	8.1	Tr.	9.4
Ephemerellidae	—	2.5	—	—	—	—	5.5	—	—	—
PLECOPTERA NYMPHS (Capniidae)	1.4	—	—	—	—	2.0	—	—	—	—
TRICHOPTERA LARVAE	—	—	13.3	1.5	5.8	—	—	47.3	5.6	9.4
Hydropsychidae	—	—	8.0	1.5	5.8	—	—	28.2	5.6	9.4
Glossosomatidae	—	—	5.3	—	—	—	—	18.8	—	—
DIPTERAN LARVAE, PUPAE	37.3	10.0	5.2	5.0	Tr.	54.3	22.2	18.3	18.1	Tr.
Chironomidae	6.8	2.5	Tr.	Tr.	Tr.	9.9	5.5	Tr.	Tr.	Tr.
WINGED INSECTS (Trichoptera)	—	—	—	3.8	—	—	—	—	14.3	—

almost as diversified as that of *Agosia chrysogaster* (38 items, Table 1), the average overlap with other fishes in Aravaipa Creek was only 44.3 percent (range 26.3 to 68.4 percent). Most foods unique to the sucker were tiny, bottom-dwelling forms such as Acarina and microcrustaceans (Table 1).

Baetid nymphs were important to *C. insignis* through much of the study, but *Tricorythodes* spp. nymphs became progressively more so and were the dominant mayfly in stomachs in January 1976 (Table 6). Abundance of *Tricorythodes* spp. nymphs in benthos and drift did not follow that same pattern. *Ephemerella* sp. nymphs were abundant in stomachs only in April, and plecopteran nymphs contributed significantly to the diet only in January 1975. The only significant trichopteran larvae were glossosomatids, present in greatest volumes in January 1976 at their peak of density in benthos.

Dipteran larvae made up the largest portion of stomach contents in January 1975 and tended to decrease in relative volume with time (Table 6). Chironomids were consistently important in stomachs of *C. insignis*, fluctuating erratically with respect to indicated availability. Simuliid larvae were significant only in the first two sampling periods.

Summer-active turbellarians were heavily used by Sonora suckers (Figs. 2–3), with some

individual fish containing them exclusively in July, the period of peak abundance of the flatworm in the benthos (Bruns and Minckley 1980).³

Of foods eaten by *C. insignis*, *Ephemerella* sp., simuliids, and glossosomatids are characteristic of swift-water habitats. Their sporadic and low occurrences in stomachs may be explained by drift into pools, where consumed, or by infrequent visits of individual suckers to riffles. Nine of the other 28 invertebrate taxa that occurred in *C. insignis*, but were too rare to quantify (Table 1), also were characteristic of swift areas. Fifteen taxa were typical of stream margins or pool-like habitats, and 4 were winged adults of aquatic insects or were derived from terrestrial sources. Diversity in pool-dwelling forms was impressive, with seven families of dipteran larvae and three groups of microcrustaceans, plus oligochaetes and nematodes.

As with *Tiaroga cobitis*, regression coefficients between some stomach contents of *C. insignis* and drift data were interestingly high, but those with benthos were low. Drifting ephemeropteran nymphs vs. stomach volumes in the same period gave $r = 0.80$, and total dipteran larvae in drift against stomach volumes was $r = 0.92$. The only benthic value to exceed $r = >0.5$ was total mayfly nymphs vs. total mayflies in stomachs ($r = 0.58$).

TABLE 6. Food habits of Sonora sucker, *Catostomus insignis*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parentheses.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (7)	Apr (3)	Jul (17)	Oct (17)	Jan (18)	Jan	Apr	Jul	Oct	Jan
Ephemeroptera nymphs	17.6	21.7	7.8	17.1	18.9	37.4	76.4	33.1	84.7	80.9
Baetidae	16.3	16.7	5.3	12.4	9.2	34.7	58.8	22.5	61.4	39.3
Tricorythidae	1.3	1.7	2.5	4.7	9.7	2.7	6.0	10.6	23.3	41.6
Ephemerellidae	—	3.3	—	—	—	—	11.6	—	—	—
Plecoptera nymphs	3.1	—	—	Tr.	Tr.	6.7	—	—	Tr.	Tr.
(Capniidae)										
Trichoptera larvae	—	Tr.	Tr.	Tr.	1.7	—	Tr.	Tr.	Tr.	7.2
(Glossosomatidae)										
Diptera larvae, pupae	26.3	5.0	4.2	1.8	2.8	56.0	17.6	17.9	8.9	11.9
Chironomidae	21.3	1.7	4.2	1.8	2.8	45.3	6.0	17.9	8.9	11.9
Simuliidae	5.0	3.3	Tr.	Tr.	Tr.	10.7	11.6	Tr.	Tr.	Tr.
Turbellaria	Tr.	1.7	11.6	1.3	Tr.	Tr.	6.0	49.0	6.4	Tr.

³Mbida Mpome, ASU (pers. comm.), has identified a parasitic fluke (Trematoda) from Aravaipa Creek catostomids that may have been confused with turbellarians in an unknown number of fish.

DESERT SUCKER.— This species (*Pantosteus clarki*) is associated with more turbulent waters in Aravaipa Creek, moving into riffles and rapids from protected places near boulders, then returning. Large adults frequent strongly flowing, deeper waters near undercut banks and obstructions, often syntopic with *Catostomus insignis*.

Although dipteran larvae were common components of diet in January and April 1975, as were turbellarians in July 1975 and baetid nymphs in January 1976, filamentous algae and diatoms made up the major portion of total foods of *Pantosteus clarki* throughout the study (Table 7, Figs. 2–3). Animal foods may well have been ingested incidental to plants. The high percentages of some animal groups on specific sampling dates, however, (e.g., turbellarians in July) indicate some degree of facultative use.

The maximum standing crops of algae in Aravaipa Creek were in April 1975 and January 1976, and they were minimal in summer and autumn, largely due to scour by summer spates (Bruns and Minckley 1980). The smallest percentages occupied by filamentous algae in *P. clarki* stomachs also were in the last two periods (Table 7). Although the dominant filamentous alga in the channel was *Cladophora glomerata*, only small quantities were ingested by the fish. Genera of algae fed upon included those eaten by *Agosia chrysogaster* (*Mougeotia* and *Spirogyra*) in trace quantities, and scarce *Rhizoclonium*, plus abundant *Oedogonium* and diatoms. The first three genera generally live along shorelines of the stream and the last two taxa are

in the channel on stones and as an abundant epiphyte of *C. glomerata*.

Diatoms also were adversely affected by spates but recovered more rapidly than did the large, attached algae, and rather consistent densities were maintained, especially in winter (Bruns and Minckley 1980, Minckley 1981). When *C. glomerata* choked the channel, *P. clarki* mouthed fronds of the alga and removed attached materials with lateral head movements and sucking action of the mouth. Stomachs contained great quantities of diatoms and *Oedogonium* at that time, and fragments of *C. glomerata* also were ingested. After scour, the sucker scraped epilithic diatom films from stones (in October, Table 7) with the cartilagenous sheaths that cover its upper and lower jaws. Fisher et al. (1981) reported similar foods for desert suckers in Sycamore Creek, Arizona.

DISCUSSION

Fishes in Aravaipa Creek present three obvious trophic patterns. The desert sucker was the only herbivore, the longfin dace was at least a facultative omnivore, and the remaining five fishes were carnivorous. A single order of insects, ephemeropterans, bore the brunt of predation by most fish species (Fig. 3).

Mayfly nymphs averaged more than 60 percent of total diets by volume in four carnivorous fishes for which quantitative data were compiled and also were eaten by the roundtail chub (Table 1) and longfin dace (Table 2). Baetid mayflies were cropped

TABLE 7. Food habits of desert sucker, *Pantosteus clarki*, from Aravaipa Creek, Arizona, 1975–1976. Organisms not occurring at more than trace (Tr. = <1.0%) amounts in any sampling period are not included; numbers of fish are in parentheses.

Food items	Percentages total stomach volumes					Percentage total food volumes				
	Jan (41)	Apr (22)	Jul (19)	Oct (21)	Jan (22)	Jan	Apr	Jul	Oct	Jan
EPHEMEROPTERA NYMPHS (Baetidae)	Tr.	Tr.	Tr.	Tr.	4.8	Tr.	Tr.	Tr.	Tr.	29.1
DIPTERA LARVAE, PUPAE	4.9	2.1	Tr.	Tr.	Tr.	19.2	21.5	Tr.	Tr.	Tr.
Chironomidae	3.8	2.1	Tr.	Tr.	Tr.	14.9	21.5	Tr.	Tr.	Tr.
Simuliidae	1.1	Tr.	Tr.	Tr.	Tr.	4.3	Tr.	Tr.	Tr.	Tr.
TURBELLARIA	—	—	1.8	—	—	—	—	22.5	—	—
ALGAE	20.6	7.6	6.2	3.8	11.6	80.8	78.5	77.6	95.6	70.9
Filamentous algae	9.3	4.6	2.9	Tr.	9.1	36.5	47.6	36.3	5.9	55.6
Diatoms	11.3	3.0	3.3	3.8	2.5	44.3	30.9	41.3	89.7	15.3

more extensively than any other group (Tables 2-7), were the most ubiquitous, and had greater biomass than other invertebrates. Occurrences of other families of mayflies in stomachs appeared to reflect differing habitat preferences of predators and prey, and seasonality of life-history phenomena of the latter. On a relative basis, mayfly nymphs remained remarkably uniform in benthic

biomass throughout the study, being reduced in relative importance by increases in hydropsychid trichopterans only in the last two sampling periods (Fig. 3). Relative importance of mayfly nymphs by weight remained uniform in drift samples. Absolute values for benthos and drift, however, varied substantially from period to period (Fig. 4). Total drift was lowest after sum-

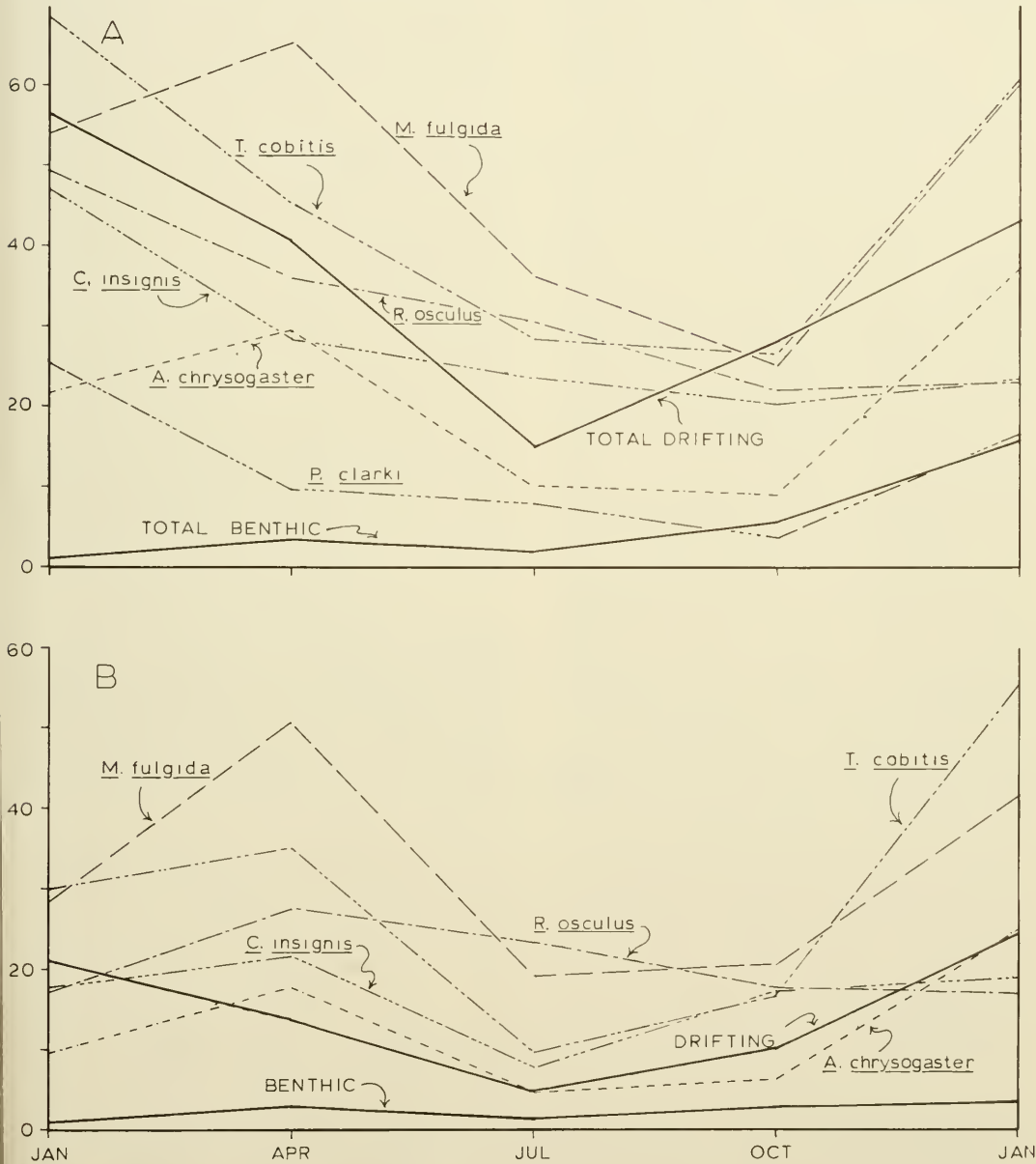


Fig. 4. Total weights of drift (mg/m³), benthos (g/m³), and percentages of total stomach volumes in six fish species for all invertebrate groups (A) and for ephemeropteran nymphs (B) from Aravaipa Creek, Arizona, 1975-1976.

mer floods in July, and benthic biomass also had declined at that time from the previous sampling period. Because mayfly nymphs dominated both benthos and drift, changes in Figure 4 result largely from adjustments in their population structure. Average weights of individual mayfly nymphs decreased in April, to remain low throughout summer as large numbers emerged and early instars were recruited into the populations. Small average sizes of baetid nymphs persisted through January 1976 in benthic samples, but a large standing crop was present and larger individuals appeared in drift (Table 8).

Preferential feeding on dipteran larvae by bottom-feeding fishes seemed indicated by data for April 1975 (Fig. 3). Dipteran larvae were relatively abundant in benthic samples at that time, although far less so than mayfly nymphs; yet they comprised a greater proportion of total stomach contents than mayflies in *Rhinichthys osculus*, *Tiaroga cobitis*, and *Catostomus insignis* (Tables 4–6, Fig. 4). Other fishes also ate substantial quantities of dipterans, but *Meda fulgida* and *Agosia chrysogaster* consumed mostly mayfly nymphs, and *Pantosteus clarki* fed heavily upon algae (Fig. 3). A relatively large year class of plecopteran nymphs also was present and was cropped by all fishes except *P. clarki*.

Each of the fishes, again excepting *P. clarki*, ate relatively greater amounts of ephemeropteran nymphs in April, perhaps exploiting the comparatively large, pre-emergence instars that were present.

Dramatic changes in stomach contents of almost all fishes occurred in July, coincident with declines in both dipteran larvae and

mayfly nymphs as a result of summer flooding (Bruns and Minckley 1980), and a substantial decrease in average individual sizes of the latter (Figs. 3–4; Table 8). Alterations in food habits consisted of a shift by 3 of the 6 fishes to different prey. Each alternate prey item increased in relative availability in July from the previous sampling period.

These changes reflected opportunistic feeding behavior of each fish species within its respective habitat. Spikedace increased its use of terrestrial organisms and winged aquatic insects, exploiting its mid- to surface water habit. A similar shift in food habits of this species was reported by Barber and Minckley (1982) in response to summer spates in Aravaipa Creek in 1966–67. Loach minnows preyed heavily upon rheophilic trichopteran larvae, in fact to a degree disproportionate to indicated abundance of that group (Fig. 3). A third fish, the Sonora sucker, amplified its cropping of bottom-inhabiting turbellarians that had commenced in April until the worms made up more than 40 percent of total stomach contents in July.

Diversification of diet was minimal in speckled dace, with a small increase in predation upon winged insects being the only apparent change in July. Perhaps this was a response to summer increases in abundance of that food source (Fig. 3). Desert suckers fed upon turbellarians, to the exclusion of other invertebrates, but this may reflect incidental intake of the abundant flatworms from riffle bottoms. Longfin dace persisted in feeding upon algae in July, along with a consistent ration of mayflies, and even showed a tendency toward eating fewer food groups in summer and autumn (Fig. 3).

TABLE 8. Mean weights of individual ephemeropteran nymphs, individual baetid ephemeropteran nymphs, and numbers of each per unit sample in benthos and drift from Aravaipa Creek, Arizona, 1975–1976.

Items	Jan	Apr	Jul	Oct	Jan
TOTAL EPHEMEROPTERA					
Benthos, wt. in mg	0.84	0.90	0.52	0.47	0.69
No/m ²	974	2,982	2,249	6,115	5,166
Drift, wt. in mg	1.58	0.58	0.51	0.44	1.00
No/m ³	13.30	25.10	9.00	22.40	22.30
BAETIDAE					
Benthos, wt. in mg	0.99	0.90	0.56	0.51	0.30
No/m ²	565	1,851	1,453	4,930	3,552
Drift, wt. in mg	1.73	0.50	0.34	0.62	1.00
No/m ³	8.40	15.70	6.70	14.90	19.20

Coincident with the return of abundant mayfly nymphs in October, average sizes of individual nymphs increased, alternate food organisms declined in abundance (in 2 instances of 3 recorded), and food habits of fishes shifted back to a pre-July condition. Dipteran larvae failed to increase to their former abundance, however, and were largely replaced in benthic biomass by trichopteran larvae. The fishes generally responded in turn, and trichopterans were consistently present in stomachs of all species except *P. clarki* in January 1976 (Fig. 3; Tables 1-7).

July percentages of total stomach volumes of all fishes decreased dramatically from April levels and remained relatively low through October (Fig. 4). Indicated availability of drift decreased in July and increased in October; benthos varied little from April through October. These declines in apparent food intake in summer and autumn may reflect physiological states of the fishes, induced by high summer temperatures, reduced reproductive activity, or other factors, as well as a change in the food base. It also may be a result of faster digestive rates (more rapid evacuation of the stomach) at higher temperatures.

SUMMARY AND CONCLUSIONS

Native fishes in Aravaipa Creek, Arizona, cropped foods relative to abundance of those foods within the system. Most fishes, excepting the single herbivore and a facultative omnivore, fed upon the same staple items, ephemeropteran nymphs, and secondarily upon trichopteran or dipteran larvae, or winged insects. The herbivore took animal foods when an item was abundant, and the omnivorous species ate almost as many nymphal mayflies, on the average, as did the carnivorous forms, but apparently selected against other invertebrates.

The degree to which diets of fishes resemble one another in a given system may have pronounced effects upon their feeding characteristics (Kawanabe 1959, Keast 1966). At times when foods are plentiful, direct effects of broad overlap in diets may be negligible. However, when foods are scarce, fishes with the greatest similarity in diet will face

increased interspecific interactions (Starrett 1950, Zaret and Rand 1971). Competition will be most severe for those species having narrow or inflexible feeding habitats (Kawanabe 1959).

Abundance of invertebrate foods in Aravaipa Creek, coupled with marked spatial partitioning of habitat by fishes present, seemed to preclude severe interspecific interactions for food. Even species with limited food habits and feeding repertoire, for example *Tiaroga cobitis*, which ate only 11 of 75 items considered available and was essentially monophagic during 4 of 5 sampling periods, seemed to have little difficulty in shifting to an alternate food source when mayflies became less abundant. Decreased total food volumes in all stomachs in July, when the major shifts in food habits occurred, may have related to decreased food supply. Stomachs remained relatively empty in October after benthos and drift increased, and shifts from alternate food supplies back to ephemeropteran nymphs had also occurred.

Mendelson (1975) similarly found that standing crops of fish food organisms appeared sufficient in Roxbury Creek, Wisconsin, to support larger fish populations than were actually present. Starrett (1950) observed that food was not an obvious limiting factor for several species of minnows in the Des Moines River, Iowa. All were able to draw from a common food base with little or no apparent competition. If direct competition for food were a significant factor in these systems, greater divergence in diets might be expected (Lawlor and Smith 1976). In situations where little partitioning of food supply by fishes appears to occur, such as in Aravaipa Creek, opportunism appears a common tendency (Mendelson 1975, Keast 1966). When a staple food decreases in abundance, a shift occurs to another locally or seasonally abundant item. Some fishes continued to feed generally upon the same foods throughout the year; others shift, each of the last to a different alternate prey. The shift by this last group of fishes implies a sophisticated spatial and behavioral adjustment that allows exploitation of an existing food base without increasing interspecific feeding interactions.

ACKNOWLEDGMENTS

M. A. Cazier, S. G. Fisher, E. Milstead, and D. I. Rasmussen read the manuscript and offered helpful suggestions and thoughtful criticisms. D. A. Bruns assisted in collection of field samples and provided information on benthos. Useful information and assistance were provided by residents of the study area and by personnel of the U.S. Bureau of Land Management and the Defenders of Wildlife. Both agencies provided continued access to the study site and supplied funds that supported parts of the research. Arizona Game and Fish Department provided permits for collection of fishes.

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NOTES ON THE REPRODUCTIVE BIOLOGY OF *ZIGADENUS PANICULATUS*, A TOXIC RANGE PLANT

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ABSTRACT.—*Zigadenus paniculatus* is a toxic plant common on sagebrush foothills at middle elevations in the western United States. Plants produce several racemes from a single stalk. Flowering commences at the base of each raceme and proceeds upwards. The terminal raceme begins blooming first and is followed by lower racemes in sequential order. Flowers are markedly protandrous and incapable of autogamy. Observations do not support the idea that apomixis is a viable reproductive strategy. Plants are mostly self-incompatible; a few seeds were produced from geitonogamous hand pollinations. The pollen/ovule ratio was high, also suggesting outcrossing as the predominant mode of sexual reproduction. A self-incompatibility mechanism may have evolved because the movements of syrphid flies on the inflorescence render protandry alone insufficient to prevent some selfing. The probable presence of toxic substances in the pollen and nectar appears to have reduced the number of potential pollinator species but increased the flower constancy of those species capable of utilizing the floral rewards.

This note describes aspects of the reproductive biology of death camas, *Zigadenus paniculatus* (Nutt.) S. Wats., a toxic range plant that occurs throughout the western United States on plains and foothills usually in association with sagebrush (*Artemisia* spp.). This perennial species commonly produces a single paniculate flowering stalk from a tunicate bulb in spring. Plants probably do not flower until the second or third year (pers. obs.). All plant parts of *Z. paniculatus* and of several other species in the genus contain numerous alkaloids through both vegetative and flowering periods (Williamson and Li 1970). Sheep are particularly susceptible to poisoning because the plant is palatable to them (Stoddart et al. 1949).

Little is known of the reproductive biology of *Zigadenus*, but two of the characteristics considered by Solbrig (1976) to favor outcrossing in plant species, i.e., the perennial habit and occurrence in environments with relatively low climatic predictability, are descriptive of *Z. paniculatus*. In addition, the smallish, creamy white, actinomorphic flowers produce both minute droplets of nectar from glands at the base of each tepal and substantial pollen, and appear adapted for outcrossing by insects. Despite the open structure of the flowers, insect visitation may be restricted to a limited subset of potential

pollinators by the presence of toxic substances (probably alkaloids). The pollen, and perhaps nectar, of at least one species (*Z. venenosus* S. Wats.) is toxic to the honey bee (*Apis mellifera* L.) (Hitchcock 1959) and possibly other potential visitors. Baker and Baker (1975) and Rhoades (1979) have hypothesized that the presence of alkaloids in flowers serves to limit visitation to flower-constant visitors and thereby increases the efficiency of the pollination system.

METHODS

A population of about 150 plants on a rocky south-facing slope at Franklin Basin, Logan Canyon, Cache National Forest (altitude 1850 m) in northern Utah was selected for study. Flowering commenced during the first week of June and continued until the end of the month.

For experimental pollination treatments, plants were precaged with chicken wire attached to wooden stakes and wrapped in Saran cloth® (Chicopee Mills, Chicopee, Massachusetts, mesh size 121/cm²) to exclude insect visitors. On each of 25 plants, one flower was used for each of five manipulations: (1) apomicty (flower emasculated before anthers dehisced); (2) autogamy (flowers unmanipulated); (3) geitonogamy (flowers

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hand-pollinated with stamens from another flower of the same plant); (4) and (5) xenogamy (flowers hand-pollinated with stamens from a distant plant) with two types of xenogamous pollinations being performed: (4) flowers with style unextended and stigmatic lobes unexposed; (5) flowers with style extended and stigmatic lobes exposed. All non-experimental flowers were removed from the plants, and the position of remaining flowers was noted. The tepals of each experimental flower were also marked with colored dots to facilitate identification. After treatment, all experimental plants were recaged.

Additional plants were collected and returned to the laboratory for examination of the sequence of floral development, and for pollen and ovule counts. The tricarpellate ovaries were dissected under a microscope and the number of ovules in each carpel counted for 10 flowers. The number of pollen grains was estimated by collecting anthers before dehiscence, drying at room temperature for two days, submerging anthers in a known volume of 70 percent alcohol, stirring vigorously with a stirring rod, and then counting grains in subsamples on a haemocytometer.

RESULTS

SEQUENCE OF FLOWER DEVELOPMENT.—The inflorescence of *Z. paniculatus* is a panicle of 3–7 racemes. Flowering begins at the base of the terminal raceme and proceeds upward. When roughly half of the flowers in the terminal raceme have reached anthesis, flowers at the base of the next highest raceme begin to open. Thus, the sequence of flowering for the entire plant proceeds from the uppermost raceme downward and flowering within a particular raceme proceeds from the base upward.

Individual flowers are protandrous and proceed through several stages. As anthesis begins, the six undehiscent swollen anthers emerge through the opening at the top of the flower caused by the parting of the petals. The petals continue to open while the filaments elongate. When the stamens are approximately three times the length of the pistil (including styles), every other anther begins dehiscing. In some cases all anthers

dehisce simultaneously. As dehiscence proceeds, the filaments begin to bend outward away from the female parts that begin extension. Up to this point, the three styles remain bent and lying atop adjacent carpels (hugging position). With dehiscence, the pistil begins to extend and the styles rise off the carpels and proceed toward erection. The spent anthers are then shed and the pistil elongates so that the styles, now bent outward, lie just below the top of the filaments. Thus, male and female phases are discrete and self-pollination within a flower is highly improbable.

POLLEN-OVULE RATIO.—The tricarpellate pistils contained between 23 and 36 ovules ($\bar{x} = 29.8 \pm 3.98$, $N = 13$), or about 10 ovules per carpel (range 6–12). Production of pollen grains by the six anthers was high ($\bar{x} = 391,666 \pm 98,456$, $N = 10$) as was the pollen-ovule ratio (13,143 grains per ovule). The high pollen-ovule ratio is another indication that the species is primarily outcrossed (Cruden 1977).

EXPERIMENTAL TREATMENTS.—Unfortunately, after all plants were tagged and experimental pollinations performed, sheep invaded the study site and trampled most plants, both caged and uncaged. Seven of the 25 caged plants were spared and data is presented for these plants only.

Flowers were neither apomictic nor autogamous; none of the seven flowers from each of these treatments produced seeds. Four of seven flowers from the geitonogamy treatments produced a total of six seeds, indicating that plants were mostly self-incompatible but not completely so.

All mature flowers that were cross-pollinated produced seed ($\bar{x} = 14.9 \pm 6.8$) and five of seven cross-pollinated before the styles were fully developed also produced some seed ($\bar{x} = 4.1 \pm 4.7$). Significantly more seed was produced by mature flowers, however (Wilcoxon Signed Rank Test, $P = 0.05$).

INSECT VISITORS.—Insect visitation to the flowers could only be recorded incidentally, but the agreement between these observations and other published studies is good. The most common visitors to *Zigadenus* in this and other studies were large, hairy syrphid flies, *Eristalis hirtus* Loew., and the solitary andrenid bee, *Andrena astragali* Viereck and

Cockerell, which seems to be a *Zigadenus* specialist (Moldenke and Neff 1974, Moldenke 1976, Hurd 1979, pers. obs.). Examination of pollen grains from the scopae of four female *A. astragali* captured on *Z. venenosus* in southeastern Wyoming in connection with another study revealed only *Zigadenus* pollen (Tepedino, unpublished). Stratiomyid flies (*Stratiomys barbata* Loew, *S. nevadae* Bigot) were also recorded occasionally. Flies were always covered with *Zigadenus* pollen. Beedlow (1979) recorded only muscid flies visiting *Z. elegans* Pursh.

DISCUSSION

Death camas possesses several characteristics that favor outcrossing as the predominant mode of sexual reproduction. Plants are primarily self-incompatible; only half the flowers that were hand-pollinated with anthers from another flower on the same plant set any seed (1–2 per flower). In addition, self-fertilization within an individual flower is most unlikely because the flowers are strongly protandrous; no flowers set seed autogamously. Low levels of autogamy were also found by Beedlow (1979) for *Z. elegans*, a late summer blooming species; only 11 of 143 bagged flowers set any seed. In contrast, Moldenke (1976) described *Zigadenus* (no species given but probably *fremontii* S. Wats.) as moderately self-compatible, but he gave no details.

Zigadenus paniculatus exhibits a pattern of flowering that may be common for plants with vertical inflorescences. Within each of the several racemes, flowering begins at the bottom and proceeds upwards. Coupled with the protandrous habit, this means that in a fully developed raceme, flowers at the bottom are functional females and those at the top are functional males. For some other plant species with single racemes and a similar sequence of floral development, bumble bee pollinators typically land at the bottom of the inflorescence and move upward, thus increasing the probability of cross-pollination and minimizing selfing (Pyke 1978 and references therein). In these species protandry is a sufficient mechanism for the avoidance of selfing and they are, in fact, self-compatible (Pyke 1978).

In *Z. paniculatus* the protandrous habit is not sufficient to avoid self-pollination because of the foraging behavior of flower-visiting flies. Syrphids and stratiomyids were commonly seen to move both between racemes on the same plant and either upward or downward within any given raceme. *Andrena astragali* was easily disturbed by observation, and movements could not be recorded with surety. Thus, if *Z. paniculatus* plants were self-compatible, as were those species studied by Pyke (1978), then much of the seed production would be due to self-pollination as effected by flies. It would seem then that incompatibility mechanisms have evolved subsequent to protandry to insure cross-pollination (Faegri and Van der Pijl 1971).

This preliminary evidence agrees with certain of the predictions of Baker and Baker (1975) and Rhoades (1979) regarding the possible function of alkaloids in floral resources. As predicted, the pollinator fauna visiting *Zigadenus* appears to be a small subset of species that are capable of foraging on the blossoms. Plant species with open blossoms typically have many more insect visitors than have been recorded for *Zigadenus*. The few common visitors to the flowers may also be highly flower constant. As mentioned above, *A. astragali* probably specializes on the collection of pollen and nectar from *Zigadenus* flowers. Syrphid flies are generally thought to be relatively inconstant in their foraging behavior (Faegri and Van der Pijl 1971), but a recent study has shown that a species of *Eristalis* can exhibit strong preferences (Kay 1978). Thus, the toxic components in *Zigadenus* pollen and nectar may indeed encourage flower constancy by pollinators (Rhoades 1979).

ACKNOWLEDGMENTS

I am grateful to both Katherine Ruggeri and Teri Peery for their meticulous help in both field and lab. Dr. Wilford E. Hansen, Utah State University, kindly confirmed Ruggeri's identifications of the flies. I thank G. E. Bohart and N. L. Stanton for comments on the manuscript.

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A NOTE ON THE FOOD OF *CALLIBAETIS* (EPHEMEROPTERA:BAETIDAE)

C. E. Cushing¹ and R. T. Rader²

ABSTRACT.— *Callibaetis* nymphs in Rattlesnake Springs, Hanford Reservation, Washington, feed almost exclusively on fine particulate organic matter (FPOM) collected from the stream bottom.

The functional group concept proposed by Cummins (1973) has become increasingly used in characterizing invertebrate fauna in streams. Inherent in categorizing aquatic organisms by various functional groups, or trophic relationships (collectors, grazers, shredders, etc.), is knowing the food eaten and how it is obtained. Merritt and Cummins (1978) have summarized a large body of information on trophic relationships of North American aquatic insects; however, the trophic relationships for the genus *Callibaetis* is unclear. This note provides information on the food habits and trophic relationships for this mayfly in Rattlesnake Springs, Washington, and supplements the Edmunds et al. (1976) note on food of this genus.

Rattlesnake Springs is a small permanent spring-stream on the U.S. Department of Energy's Hanford Reservation in south-central Washington. The region is in the northern extension of the Great Basin. Base flow is about 0.011 m³/s, and the stream flows about 3 km before disappearing into the desert floor. Further physical, chemical, and biological data can be found in Cushing et al. (1980) and Cushing and Wolf (in press).

METHODS

Callibaetis nymphs were collected with hand nets during a sampling program to characterize the invertebrate fauna of Rattlesnake Springs. Samples were preserved in 70 percent ETOH until examination. Gut contents were analyzed by suspension, filtration, and microscopic examination essentially as described by Cummins (1973), Gray and

Ward (1979), and Short and Ward (1981). The majority of the particles were spherical; hence, volumetric calculations were based on the particle size diameters.

RESULTS AND DISCUSSION

Data for 31 nymphs from eight sites are presented in Table 1. The number of organic detrital particles per nymph gut ranged from 3270 to 17,600, and varied in size from 111 μ m to 230 μ m. These particles comprised from 95 to 100 percent of the material present, by number; diatoms comprised 1 to 5 percent, and insect parts, probably ingested by chance, less than 1 percent. The calculated volume of the particles per nymph ranged from 7.6 to 22.3 mm³.

Stations 1 through 17 are in the open desert, and 27, 29, and 31 are in a steep-sided canyon. The unusually high number of particles in the guts of nymphs from Sta. 31 may be related to its location. It is located at the origin of Rattlesnake Springs in a seepage pool with heavy growths of filamentous green algae.

These data indicate that *Callibaetis* is primarily a collector-gatherer (sensu Cummins 1973) feeding mainly on fine particulate organic matter (FPOM) from the stream bottom. These results are in contrast to Edmunds et al. (1976), who state that *Callibaetis* nymphs are herbivorous, feeding on diatoms and other algae. A rich diatom and algal flora is present in Rattlesnake Springs (Lippert and Cushing 1973); yet these forms make up less than 5 percent of the food ingested in Rattlesnake Springs. The findings are, however,

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consistent with data on other Baetidae (Cummins 1973, Merritt and Cummins 1978).

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TABLE 1. Detrital (FPOM) particles in *Callibaetis* guts taken during July 1980.

Date	Station	n	\bar{x} No. particles (range)	\bar{x} diameter, μ m (range)	Part. volume, mm ³
7 July	1	4	5300 (3440-7070)	140 (110-200)	7.6 ¹
8 July	9	4	6600 (5700-7190)	170 (120-210)	17.0
8 July	11	4	3940 (3270-4330)	210 (170-230)	16.5
9 July	17	4	7300 (4900-9090)	150 (130-190)	12.9
10 July	23	3	5300 (4900-5600)	190 (160-210)	19.0
10 July	27	4	7400 (5070-9660)	140 (120-170)	10.6
14 July	29	4	8900 (5750-11,600)	150 (120-200)	15.7
14 July	31	4	15,500 (10,500-17,600)	140 (110-170)	22.3

¹Volume calculated using mean numbers for particle size and numbers. Because FPOM constitutes 95 to 100 percent of the gut contents observed, similar data for diatoms and insect parts were not calculated.

SUBAERIAL ALGAE OF NAVAJO NATIONAL MONUMENT, ARIZONA

Jeffrey R. Johansen¹, Samuel R. Rushforth², and Jack D. Brotherson²

ABSTRACT.— Samples from soils and other xeric substrates in Navajo National Monument, Navajo County, Arizona, were collected in 1978. After being moistened with deionized water for three days, these samples were analyzed for algae. Thirty algal taxa were identified. Five species of filamentous Cyanophyta comprised the majority of the biomass. Diatoms were ubiquitous in the soils although low in density. Diatom floras were very similar throughout the monument. Well-developed algal crusts were common in sites where grazing and excessive litter were absent.

Cryptogamic soil crust communities in arid regions of the world have received attention from several workers (Ali and Sandhu 1972, Anantani and Marathe 1974a, 1974b, Bischoff and Bold 1963, Cameron 1964, Chantanachai and Bold 1962, Durrell 1959, Fletcher and Martin 1948, Forest and Weston 1966, Hayek and Hulbary 1956). Such communities are variable in composition. Those best developed form crusted hummocks composed of as many as 30 to 40 species of various cryptogams including lichens, mosses, and algae (Anderson and Rushforth 1976). Under some circumstances such crusts do not develop, but algae may still be present and bind soil particles (Durrell and Shields 1961). Algal binding and crust formation protect the soils from heavy summer rains and persistent winds (Anderson and Rushforth 1976). In addition to reducing erosion and consequent leaching of minerals, nitrogen fixation by some of the blue-green algae also contributes to overall soil quality (Macgregor and Johnson 1971, Rychert and Skujins 1974, Shields and Durrell 1964, Snyder and Wullstein 1973). When crusts are disturbed by grazing or heavy human traffic, the binding of the soil is decreased and soil erosion increases (Anderson, Harper, and Rushforth in press, Loope and Gifford 1972).

Cryptogamic crusts are very widespread and important in arid regions of western North America and have been under investigation in our laboratory for several years. Anderson et al. (1976, in press) examined soil crusts throughout Utah, and

discussed taxonomy, distribution, and the effects of grazing and soil quality on crust development. The present study is a continuation of our cryptogamic research and deals with the algal component of the soils and subaerial substrates of Navajo National Monument, Navajo County, Arizona.

Navajo National Monument is located in northeastern Arizona about 16 km north and west of Black Mesa and Arizona Highway 160. The principal sites of the monument are three large Indian "cliff dwellings" of the Anasazi culture. These cliff dwellings are located in three separate canyons. Betatakin and Keet Seel Canyons are part of the Tsegi Canyon complex and Inscription House is located about 32 km west of Betatakin in Nitsin Canyon. All three units lie in country dominated by pinyon-juniper communities (*Pinus edulis*, *Juniperus osteosperma*) growing in soil pockets associated with sandstone slickrock (Fig. 1). Within the region there exist many deep-cut canyons with high-walled sandstone cliffs, often reaching heights of 300 m above the streambeds. Springs and seeps are often encountered in these canyons, creating unique habitats that develop plant and animal communities foreign to the overall pinyon-juniper type. Aspen (*Populus tremuloides*), Gambel oak (*Quercus gambelii*), and Douglas-fir (*Pseudotsuga menziesii*) communities are present in Betatakin Canyon; oak and mixed weed communities (Fig. 2) are present in Keet Seel; and a large, heavily grazed, annual weed community (Fig. 3) exists in the Inscription House segment (Brotherson et al. 1978, Brotherson et al. in review).

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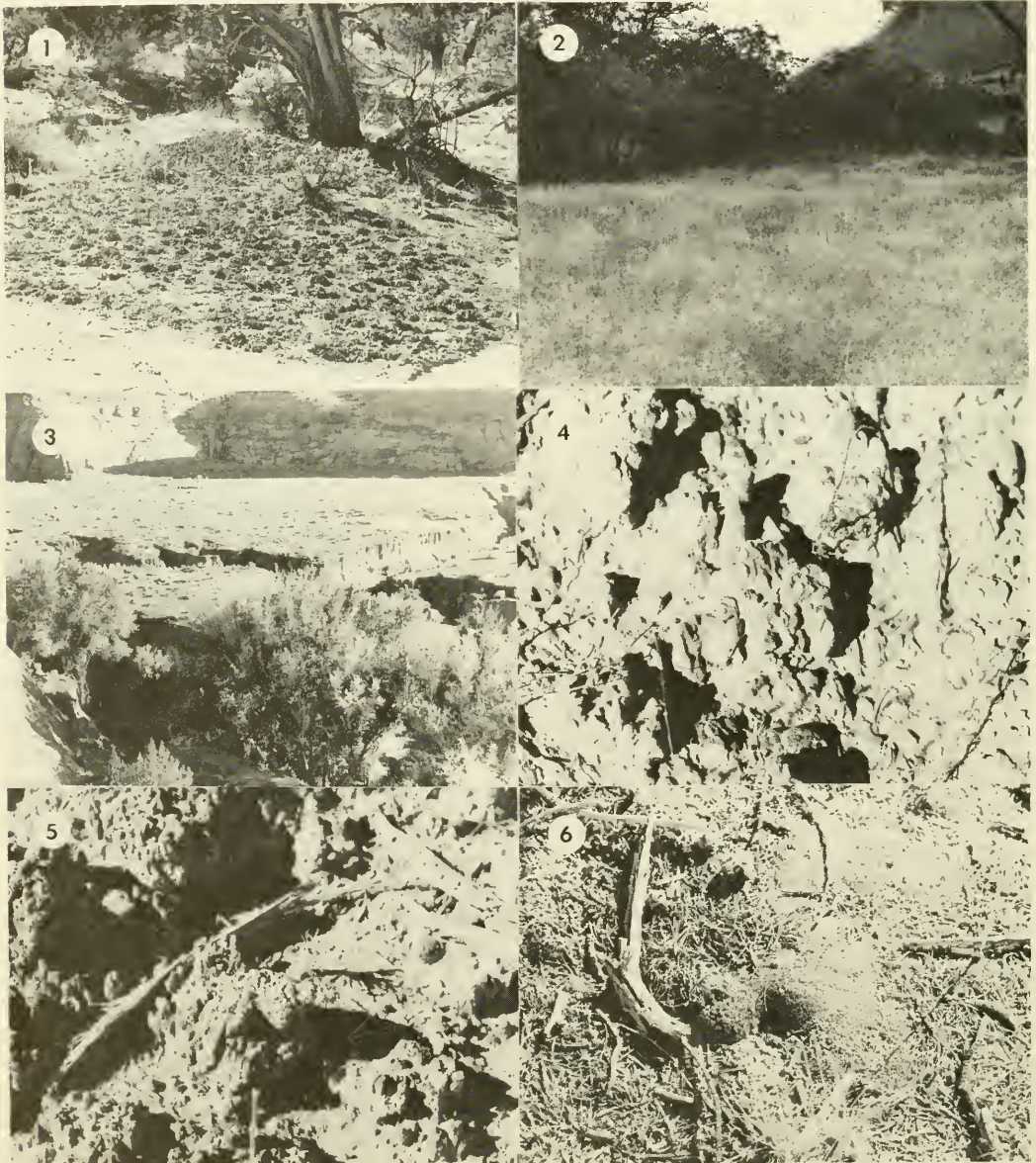
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The soils of Navajo National Monument are essentially all derived from the Navajo sandstone formation. Even so, many environmental subtypes exist, providing different habitats for the development of cryptogams.

MATERIALS AND METHODS

Soil samples from the communities discussed above were obtained during the sum-

mer of 1978 by scooping approximately 200 g of soil into collection boxes. In addition mosses, lichens, and evident cryptogamic crusts (Fig. 4-6) growing on soils, rocks, and trees in the monument were also collected. These samples were subsequently moistened for 36 hours with distilled water to hydrate prominent living algae. Permanent diatom slides were later prepared using standard acid



Figs. 1-6. Collecting sites and cryptogamic crusts in Navajo National Monument, Arizona: 1, Cryptogamic soil crusts in pinyon-juniper slickrock community of Betatakin; 2, Mixed weed and oak communities of Keet Seel; 3, Annual weed community in heavily eroded Nitsin Canyon, Inscription House; 4, Algal crust; 5, Lichen crust; 6, Moss crust.

oxidation techniques and Naphrax mountant (St. Clair and Rushforth 1976). All species were studied and identified using a Zeiss RA research microscope with Nomarski interference and phase-contrast accessories.

RESULTS AND DISCUSSION

A total of thirty algal taxa were found in the soil and rock substrates of the monument. Ten of these were blue-green algae (Cyanophyta, Fig. 7-17, 19, 20), one was a green alga (Chlorophyta, Fig. 18), and 19 were diatoms (Bacillariophyta, Fig. 21-41). These taxa are listed in Table 1 together with pertinent descriptive data. The algae most prevalent in crusted soils were all filamentous blue-green species; *Anabaena variabilis*, *Microcoleus vaginatus*, *Nostoc muscorum*, *Phormidium tenue*, and *Scytonema myochrous* (Table 2). These algae, particularly *M. vaginatus*, were chiefly responsible for binding the soil and producing crusts.

The best-developed crusts were those in the pinyon-juniper communities of Betatakin (Fig. 1). These soils have been protected from grazing for many years and the crusts here

TABLE 1. Algal taxa observed in sample collections from selected terrestrial environments of Navajo National Monument. Pertinent descriptive information for each species is included.

CYANOPHYTA

Anabaena variabilis Kütz. (Fig. 12): cells 4 μ m wide by 2-4 μ m long; heterocysts 7 μ m wide by 6 μ m long.

Chlorogloea fritschii Mitra (Fig. 9): cells 4-6 μ m in diameter.

Chroococcus rufescens (Kütz.) Naeg. (Fig. 7): colony 10-25 μ m in diameter; cells 3-11 μ m in diameter.

Chroococcus turgidus (Kütz.) Naeg. (Fig. 8): colony 18-20 μ m wide by 20-25 μ m long; cells 6-13 μ m in diameter.

Lyngbya linnetica Lemm. (Fig. 10): cells 1-3 μ m wide by 1.6-6 μ m long.

Microcoleus vaginatus (Vauch.) Gomont (Figs. 19, 20): colonial sheath 20-32 μ m wide; trichomes 2.5-8 μ m wide; cells 2-9 μ m long.

Nostoc commune Vauch. (Figs. 13, 14): colony microscopic; cells 4-5 μ m wide by 4-6 μ m long; heterocysts 6-8 μ m in diameter; akinetes 6 μ m wide by 8 μ m long.

Nostoc muscorum C. A. Ag. (Fig. 15): colony microscopic; cells 2.5-4 μ m in diameter; heterocysts 6 μ m in diameter.

Table 1 continued.

Phormidium tenue (Menegh.) Gomont (Fig. 11): cells .7-2.5 μ m wide by 2-3 μ m long.
Scytonema myochrous (Dillw.) C. A. Ag. (Figs. 16-17): filaments 12-15 μ m wide; trichomes 6-12 μ m wide; cells 3-12 μ m long; heterocysts 10-12 μ m wide by 7.5-10 μ m long.

CHLOROPHYTA

Unknown coccoid green alga (Fig. 18): cells spherical, 6-15 μ m in diameter.

BACILLARIOPHYTA

Achnanthes linearis W. Sm. (Fig. 24): valve 2.5 μ m wide by 9 μ m long; striae 24 in 10 μ m in the center to about 30 in 10 μ m near the ends.

Achnanthes microcephala (Kütz.) Grunow: valve 3.5 μ m wide by 18 μ m long; striae 26-30 in 10 μ m, becoming finer towards the ends.

Caloneis bacillum (Grun.) Cl. (Fig. 36): valve 3.5-4.5 μ m wide by 14-24 μ m long; striae 20-22 in 10 μ m.

Cyclotella comta (Ehr.) Kütz. (Fig. 22): valve 30 μ m in diameter; striae 10 in 10 μ m.

Cymbella turgida (Greg.) Cl.: valve 10 μ m wide by 33 μ m long; striae 8-9 in 10 μ m.

Denticula elegans f. *valida* Pedic. (Figs. 40, 41): valve 4-6 μ m wide by 24-30 μ m long; costae 3-4 in 10 μ m; striae 20 in 10 μ m.

Diatoma vulgare Bory (Fig. 26): valve 12 μ m wide by 29 μ m long; costae 7 in 10 μ m; striae unresolved.

Hannaea arcus (Ehr.) Patr.: valve 6 μ m wide; striae 12 in 10 μ m (identified from broken specimens).

Hantzschia amphioxys (Ehr.) Grunow (Figs. 37-39): valve 6-9 μ m wide by 29-35 μ m long; fibulae 6-9 in 10 μ m; striae 21-25 in 10 μ m.

Melosira roeseana Rabh. (Figs. 21, 25): frustule 12-19 μ m in diameter by 16-24 μ m long; striae 7-9 in 10 μ m.

Navicula mutica Kütz. (Figs. 27, 28): valve 6-9 μ m wide by 20-29 μ m long; striae 18-20 in 10 μ m.

Navicula mutica var. *cohnii* (Hilse) Grunow (Fig. 29): valve 5-8 μ m wide by 9-21 μ m long; striae 18-20 in 10 μ m.

Navicula mutica var. *undulata* (Hilse) Grunow (Fig. 30): valve 6 μ m wide by 13-19 μ m long; striae 16 in 10 μ m.

Navicula tripunctata (O. F. Müll.) Bory (Fig. 32): valve 7 μ m wide by 31 μ m long; striae 12-14 in 10 μ m.

Navicula tripunctata var. *schizonemoides* (V. H.) Patr. (Fig. 33): valve 7 μ m wide by 36 μ m long; striae 11-12 in 10 μ m.

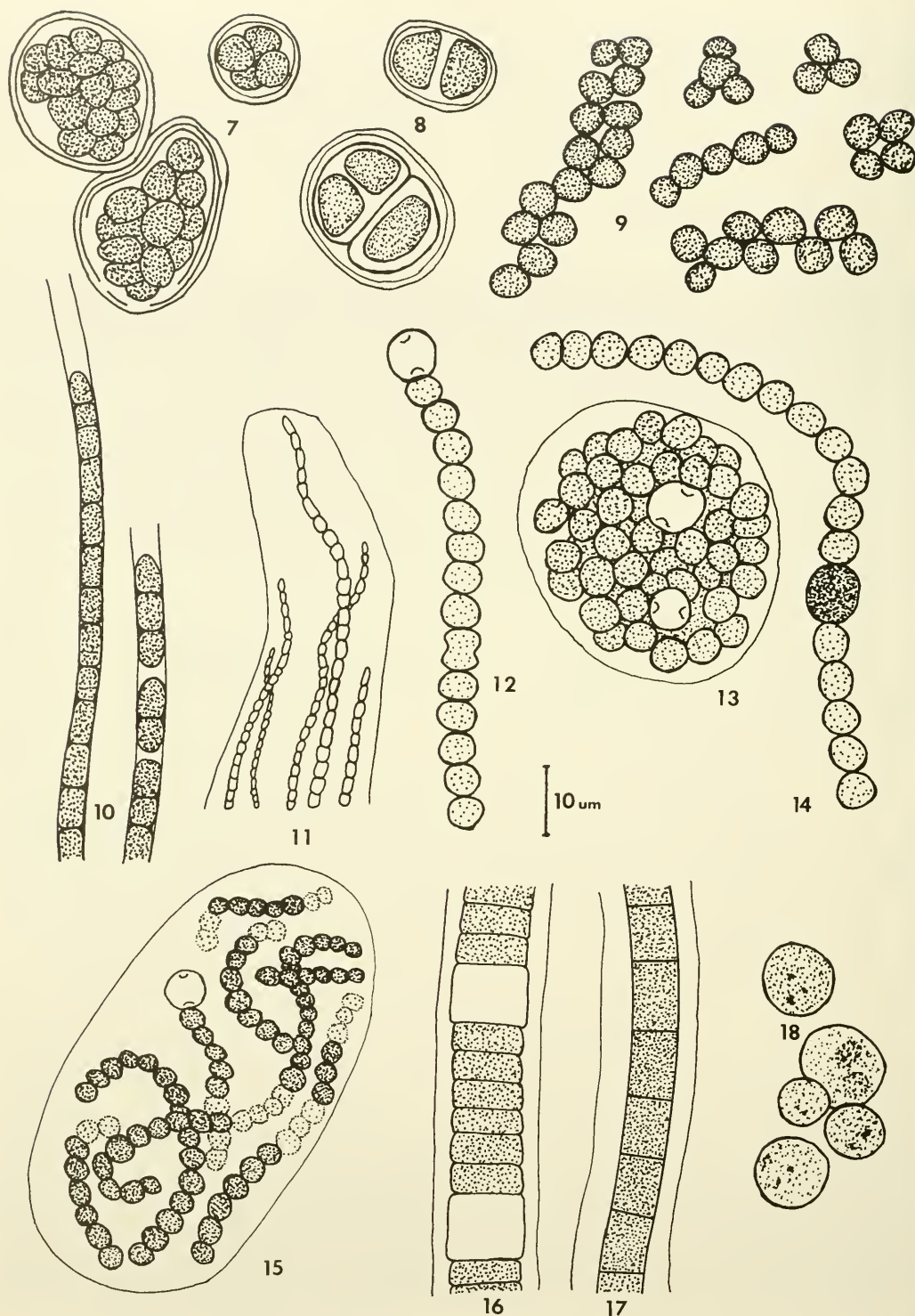
Navicula species (Fig. 31): valve 3-4 μ m wide by 15-18 μ m long; striae 20-22 in 10 μ m in the center, becoming finer towards the ends.

Pinnularia appendiculata (C. A. Ag.) Cl. (Fig. 35): valve 4.5-6 μ m wide by 21-32 μ m long; striae 16-19 in 10 μ m.

Pinnularia borealis Ehr. (Fig. 34): valve 7-8 μ m wide by 29-45 μ m long; striae 4-5 in 10 μ m.

Pinnularia microstauron (Ehr.) Cl.: valve 11 μ m wide by 54 μ m long; striae 11 in 10 μ m.

Stephanodiscus astraea var. *minutula* (Kütz.) Grunow (Fig. 23): valve 18 μ m in diameter; striae 12 in 10 μ m.



Figs. 7-18. Algae of xeric substrates in Navajo National Monument. All illustrations are drawn to the same scale: 7, *Chroococcus rufescens*; 8, *Chroococcus turgidus*; 9, *Chlorogloea fritschii*; 10, *Lyngbya limnetica*; 11, *Phormidium tenue*; 12, *Anabaena variabilis*; 13, 14, *Nostoc commune*; 15, *Nostoc muscorum*; 16, 17, *Scytonema myochrous*; 18, Unknown coccoid green alga.

often contain mosses and lichens in addition to algae. The oak, fir, and aspen communities of Betatakin are covered with excessive litter, which retards crust production. Due to overgrazing, crusts were absent in the Keet Seel and Inscription House areas, and serious erosion problems were evident (Fig. 3). Some crusts were found in the slickrock above Inscription House, however, where soil pockets in the rock were not subjected to grazing.

The most surprising find of this study was the widespread distribution of diatoms in the xeric habitats in the monument (Table 3). Though not a major part of the algal biomass, diatoms were found in every sample taken. The uncrusted soils of Keet Seel contained few blue-green and green algae, yet hosted a diverse diatom flora. Likewise, the lichens on the oaks in Keet Seel had diatoms associated with them, including *Hannaea arcus*, which was not seen elsewhere in the monument. The mosses and lichens on rock surfaces also supported diatom assemblages. Soils from the heavily grazed area of Inscription House had a very depressed diatom population, with only four frustules being seen after extensive examination of samples. All uncrusted soils of

Betatakin, though poor in filamentous algae, contained numerous diatoms.

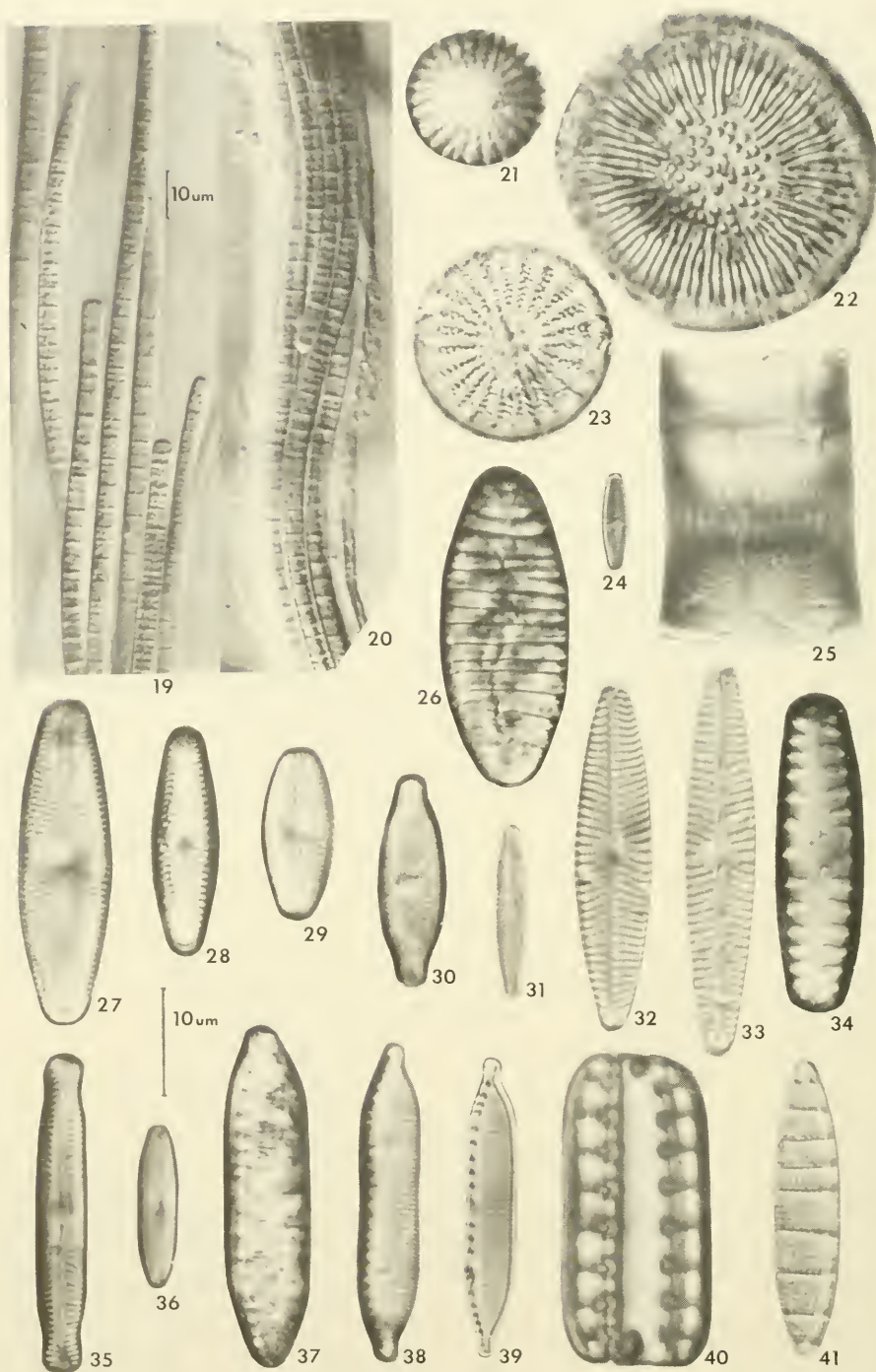
Hantzschia amphioxys was the most abundant diatom, with *Navicula mutica* var. *cohnii* being nearly as abundant (Table 3). *Navicula mutica*, *Pinnularia borealis*, and *Caloneis bacillum* were also important. The presence of two centric planktonic diatoms, *Cyclotella comta* and *Stephanodiscus astraera* var. *minutula*, was somewhat surprising, though these taxa have been reported from arid soils elsewhere (Anderson and Rushforth

TABLE 2. Distribution of soil nondiatoms in Navajo National Monument. Crusted soils (C), uncrusted soils (U), rocks (R), and trees (T) were sampled. Upper case letters represent common to abundant taxa and lower case letters represent rare to infrequent taxa.

Species	Betatakin	Keet Seel	Inscription House
CYANOPHYTA			
<i>Anabaena variabilis</i> Kütz.	Cu		c
<i>Chlorogloea fritschii</i> Mitra	c		R
<i>Chroococcus rufescens</i> (Kütz.) Naeg.	u		c
<i>C. turgidus</i> (Kütz.) Naeg.	r		cR
<i>Lyngbya linnetica</i> Lemm.	c		
<i>Microcoleus vaginatus</i> (Vauch.) Gomont	Cu		Cr
<i>Nostoc commune</i> Vauch.			c
<i>N. muscorum</i> C. A. Ag.	C		C
<i>Phormidium tenue</i> (Menegh.) Gomont			C
<i>Scytonema myochrous</i> (Dillw.) C.A. Ag.	C		Cr.
CHLOROPHYTA			
Unknown coccoid green alga	cu	ut	r

TABLE 3. Distribution of soil diatoms in Navajo National Monument. Crusted soils (C), uncrusted soils (U), rocks (R), and trees (T), were sampled. Upper case letters represent relative density 20 percent or above and lower case letters represent relative density less than 20 percent.

Species	Betatakin	Keet Seel	Inscription House
BACILLARIOPHYTA			
<i>Achnanthes linearis</i> W. Sm.	cu		u
<i>A. microcephala</i> (Kütz.) Grun.	r	u	
<i>Caloneis bacillum</i> (Grun.) Cl.	cur		cur
<i>Cyclotella comta</i> (Ehr.) Kütz.	cu		
<i>Cymbella turgida</i> (Greg.) Cl.			r
<i>Denticula elegans</i> f. <i>valida</i> Pedic.	cr	u	cu
<i>Diatoma vulgare</i> Bory	cu		
<i>Hannaea arcus</i> (Ehr.) Patr.		t	
<i>Hantzschia amphioxys</i> (Ehr.) Grun.	CUR	UT	CUR
<i>Melosira roseana</i> Rabh.	r	u	c
<i>Navicula mutica</i> Kütz. (Hilse) Grun.	cU	u	cur
<i>N. mutica</i> var. <i>cohnii</i> (Hilse) Grun.	Cur	U	CUR
<i>N. mutica</i> var. <i>undulata</i> (Hilse) Grun.			c
<i>N. tripunctata</i> (O. F. Mull.) Bory			u
<i>N. tripunctata</i> var. <i>schizonemoides</i> (V. H.) Patr.	r		
<i>Navicula</i> species	cur	u	u
<i>Pinnularia appendiculata</i> (C. A. Ag.) Cl.	ur	u	u
<i>P. borealis</i> Ehr.	cUr		cur
<i>P. microstauron</i> (Ehr.) Cl.			r
<i>Stephanodiscus carconensis</i> var. <i>pusilla</i> Grun.			c



Figs. 19–41. Algae of xeric substrates in Navajo National Monument. All diatom micrographs are enlarged to the same magnification: 19, 20, *Microcoleus vaginatus*; 21, *Melosira roeseana*; 22, *Cyclotella comta*; 23, *Stephanodiscus astraea* var. *minutula*; 24, *Achnanthes linearis*; 25, *Melosira roeseana*; 26, *Diatoma vulgare*; 27, 28, *Navicula mutica*; 29, *Navicula mutica* var. *cohnii*; 30, *Navicula mutica* var. *undulata*; 31, *Navicula* species; 32, *Navicula tripunctata*; 33, *Navicula tripunctata* var. *schizonemoides*; 34, *Pinnularia borealis*; 35, *Pinnularia appendiculata*; 36, *Caloneis bacillum*; 37–39, *Hantzschia amphioxys*; 40, 41, *Denticula elegans* f. *valida*.

1976). It is interesting to note that neither of these species was observed in the aquatic habitats of the monument.

The close similarity of diatom floras in the soils of the monument is good evidence that the diatoms encountered in the samples represent living communities, not incidental contaminants. Upon examining moistened crusts, living diatoms were rare. Numerous frustules, however, were found approximately 1 cm below the soil surface. It is likely that the diatoms migrate to the soil surface under favorable conditions. More work is planned to test this hypothesis. The discovery that algae grow in very arid sandy soils that show no evidence of crusting or binding has stimulated our interest in such soils, and research on the various uncrusted soil types in arid western North America is planned. Furthermore, we are currently studying the effects of grazing and compaction by humans on cryptogamic communities.

ACKNOWLEDGMENTS

This research was funded in part by the National Park Service, Southwest Region, Grant PX 7029-8-0570, and the Department of Botany and Range Science, Brigham Young University. We thank the personnel at Navajo National Monument for their help and courtesy.

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HISTORY AND STATUS OF THE FRANKLIN'S GULL ON MALHEUR NATIONAL WILDLIFE REFUGE, OREGON

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ABSTRACT.— Franklin's Gulls first arrived in southeast Oregon in 1943, but the first nest was not located until 1948. From 1949 to 1964 gull numbers showed annual fluctuations. An increase began in 1965 and continued through 1980. By 1980 an estimated 2500 Franklin's Gulls were nesting on Malheur National Wildlife Refuge, Harney County, Oregon. The species arrives in April and nesting begins by 1 June. Average nest and egg measurements were similar to those from other areas within the species range.

The present breeding distribution of the Franklin's Gull (*Larus pipixcan*) is from southeast Alberta, central and southern Saskatchewan, and southwestern Manitoba; south to central-eastern Oregon, south-central Montana, northwest Utah, eastern North Dakota, northeastern South Dakota, southwestern Minnesota and northwestern Iowa (AOU Check-list 1957). Malheur National Wildlife Refuge (NWR), Harney County, Oregon, is the western extremity of the species' breeding range.

The Franklin's Gull was first observed in southeastern Oregon in 1943, about the same time the species appeared in Idaho. Burleigh (1972) reported that until 1941 the species was only a straggler in southern Idaho, but is now a local summer resident.

The range extension is further illustrated by the gulls' distribution given in the 1931 AOU Check-list. The check-list recorded the species as a breeding bird in the prairie regions of interior North America across its present range, but was not listed as a straggler in Oregon or Idaho.

The history of Franklin's Gulls in south-central Oregon with limited data on its breeding biology, is presented here.

STUDY AREA

Malheur NWR is in the southern part of the Malheur-Harney Lakes Basin, about 40 km south of Burns, Oregon, in the northern extremity of the Great Basin (Fig. 1). The refuge consists of about 73,655 ha of large lakes,

alkali flats, wet meadows, extensive freshwater marshes and sagebrush uplands. The climate is semiarid and water is supplied from direct precipitation and runoff from the surrounding watersheds via the Blitzen and Silvies rivers, and Silver Creek.

For Franklin's Gulls, the most important part of the refuge is Malheur Lake. The lake is one of the largest freshwater marshes in the United States. According to refuge files, the size of the marsh varies from year to year, and during the past 45 years has averaged about 18,200 ha, ranging from a low of 200 ha (1961) to 27,125 ha (1980). Water rarely exceeds 2 m in depth. Hardstem bulrush (*Scirpus acutus*) is the dominant emergent plant, but along the lake's periphery, broad-fruited burreed (*Sparganium eurycarpum*) and baltic rush (*Juncus balticus*) are locally abundant (Duebber 1969).

Franklin's Gulls feed in the meadows that surround the lake, and use the deeper water of the lake for nesting. Limited feeding also occurs in the surrounding uplands and plowed fields in June and July, when grasshoppers are abundant.

HISTORY

Oregon's first recorded Franklin's Gull was seen at Malheur NWR on 24 April 1943 (refuge files). It is unknown to us why the species invaded southeast Oregon. Agricultural development, such as cereal grains, row crops, and alfalfa, along the Snake River in southern Idaho could have facilitated this invasion.

¹U.S. Fish and Wildlife Service, Box 113, Burns, Oregon 97720.



Fig. 1. Malheur National Wildlife Refuge, Oregon, in relation to the Great Basin.

Franklin's Gulls, like some other gulls, are well adapted to agricultural developments and tend to seek newly plowed fields, where they feed on invertebrates exposed by farm machinery. This association with human activity could have allowed the species to move westward from its nearest known nesting colony in northern Utah (AOU Check-list 1931).

The species was regularly seen on Malheur NWR during the breeding season after 1943 and was believed nesting in 1947. The first nest was not located until 7 June 1948. This floating nest contained three eggs and was composed of hardstem bulrush. The water depth was 1.2 m and about six other Franklin's Gull pairs were circling over the area.

From 1949 through 1961, Franklin's Gull numbers showed annual fluctuations that appeared to be strongly associated with the productivity of Malheur Lake (Table 1). Only 30 to 40 individual gulls nested on the refuge from 1949 through 1951, but in 1952 their numbers increased to 250. The lake dropped after 1952, reaching a low point of 14,570 ha in 1955. The number of gulls likewise decreased during this period. By the fall of 1955 Franklin's Gulls numbers had dropped to 80 individuals. Also, during this period the introduced carp (*Cyprinus carpio*) had increased to such great numbers that in the fall of 1955 the lake was chemically treated to reduce their population. The spraying of the lake with rotenone resulted in an estimated kill of 1.5 million carp.

TABLE 1. Individual Franklin's Gull numbers on Malheur National Wildlife Refuge, Oregon.

Year	Estimated number	Year	Estimated number
1949	40	1965	500
1950	40	1966	500
1951	30	1967	500
1952	250	*1968	700
1953	100	1969	550
1954	100	1970	1000
*1955	80	1971	1200
1956	300	1972	1000
1957	100	1973	2000
1958	50	1974	2000
1959	100	1975	0
1960	50	1976	400
*1961	10	*1977	500
1962	150	1978	850
1963	150	1979	2200
1964	150	1980	2500

*Years of chemical treatment for carp in Malheur Lake.

Above normal runoff in 1956 increased the lake size to 22,600 ha and submergent plants returned and grew to cover 6070 ha. Gulls likewise responded to this increase and 300 individuals nested in 1956. High lake levels (26,710 ha) were also reported in both 1957 and 1958, but for undetermined reasons numbers declined to 100 and 50 gulls, respectively.

Drought conditions began in 1959 (driest year since 1934) and continued through 1961 when the lake reached the lowest level it had been in 25 years. By the fall of 1961 only 200 ha of water remained and carp were again chemically treated, resulting in an estimated kill of 150,000 carp. In 1961, only 10 Franklin's Gulls were present in the nesting colony. Gulls began to increase in 1962, with 150 individuals nesting in Malheur Lake. They increased to record levels from 1965 through 1968, with 700 individuals nesting in 1968. By 1970 the nesting population reached 1000 individuals for the first time. From 1970 through 1974 the estimated nesting population ranged from 1000 to 2000 individuals.

In 1975, the species arrived on schedule and remained in the Malheur-Harney Lake Basin throughout the nesting season. By late May there were an estimated 2130 gulls in the basin, but only 50 on Malheur Lake. Most of the birds remained in the irrigated meadows south and east of Burns. They did not nest in Malheur Lake in 1975, although there was a small colony located off the refuge about 8 km northwest of the former lake colony. A possible explanation for the lack of Franklin's Gulls nesting on Malheur Lake in 1975 was carp populations had greatly reduced the aquatic invertebrate populations by reducing the aquatic plant production. Gulls probably did not attempt to nest, because invertebrates are the principal food for nesting Franklin's Gulls.

Although the lake was still overpopulated with carp in 1976, about 400 gulls nested and in 1977 500 nested; in 1977, however, no nests were successful. The lake was in a relatively unproductive state with high carp populations, low lake levels (6100 ha), and only 816 ha of submergent vegetation. Carp control was subsequently accomplished in the fall of 1977, resulting in an estimated kill of

3.5 million carp. Conditions improved in 1978, when 850 gulls successfully nested, increasing to 2500 in 1980.

BREEDING BIOLOGY

The Franklin's Gull mean arrival date in southeastern Oregon is 23 April, with the earliest record being 11 April 1970. The species is usually seen first at Malheur Lake on potential nesting sites, or adjacent to the lake near Malheur NWR headquarters. If the lake is in poor condition, with high carp populations, or low lake levels, gulls may first appear in the irrigated meadows south and east of Burns.

The majority of breeding gulls have arrived in the basin by 10 May and have begun to nest by 1 June. The species usually nests in scattered stands of bulrush, avoiding dense stands. Bulrush density has varied from year to year in Malheur Lake, and this has contributed to shifts in colony sites. Burger (1974) reported that nesting Franklin's Gulls in northwest Minnesota also avoided dense emergent growth.

On 14 and 16 June 1969, E. L. McLaury and C. D. Littlefield examined 51 nests in a large gull colony in the central part of the lake. The nests consisted of mounds of dried bulrush over 76 cm of water. Average nest measurements were as follows: nest height 18 cm, basal diameter 86 cm, crown diameter 23 cm, bowl diameter 16 cm, and bowl depth 4.3 cm. A total of 100 eggs was measured and averaged 51.3×36.3 mm (range 46.5–55.6 mm; 34.2–37.8 mm). Our data on egg measurements is similar to that reported by Roberts (1900), Gaay (1968), and Burger (1973). On 27 May and 9 June 1980, 10 nests were examined by S. P. Thompson and J. E. Cornely. These nests were over 169 cm of water. Average nest measurements were as follows: nest height 17 cm, basal diameter 63 cm, crown diameter 21 cm, bowl diameter 15 cm, and bowl depth 6.3 cm.

Nesting success at Malheur NWR was determined for 48 nests in 1969. Any nest that had at least one egg that hatched was considered successful. Of these, 45 were successful (93.7 percent), and 3 were unsuccessful (6.3 percent).

CONCLUSIONS

Franklin's Gulls became established on Malheur NWR in the late 1940s. At present the species is well established in southeast Oregon. Its status should remain the same unless Malheur Lake becomes unproductive for a sustained period.

Carp, which were introduced into the basin in the early 1920s, have decreased productivity of the lake since the early 1950s. Chemical application of rotenone in 1955, 1961, 1968, and 1977 resulted in large numbers of carp being killed. Usually within five years carp populations have become reestablished. In years when carp numbers were high, numbers of nesting Franklin's Gulls usually declined. Adults feed in the surrounding meadows, but little food is available near the colonies. As young approach fledging, the adults spend less time with them (Burger 1974) and food becomes a limiting factor.

Presently, the local population of gulls is increasing, but as chemical prices continue to spiral upward, carp control could become an impossibility. Such a situation could affect the Franklin's Gull population on the refuge and in southeast Oregon.

ACKNOWLEDGMENTS

We thank John Cornely, Brad Ehlers, Joseph Mazzoni, and Caryn Talbot for reviewing the manuscript, and Ruth Warneke for typing assistance. Further, we would especially like to thank Eldon McLaury, who stimulated interest in conducting field work on the Franklin's Gull at Malheur NWR.

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OPHIOTAENIA CRITICA (CESTODA: PROTEOCEPHALIDAE), A PARASITE OF THE COLORADO RIVER SQUAWFISH

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ABSTRACT.— A total of 19 cestodes, *Ophiotaenia* sp., were recovered by deworming from adult Colorado River Squawfish (*Pteichocheilus lucius*) maintained at the U.S. National Fish Hatchery at Willow Beach, Arizona. These specimens differ from other described species and are named *Ophiotaenia critica*.

Reports concerning the helminth parasites of native Arizona fishes are limited. Unfortunately, some hosts, such as the Colorado River Squawfish, *Pteichocheilus lucius*, are currently considered endangered and hence are difficult to examine for their parasitic fauna. Vanicek and Kramer (1969) reported the proteocephalid tapeworm *Proteocephalus ambloplitis* from *P. lucius* and *Gila robusta*. Buckner (1972) reported the proteocephalid *Ophiotaenia fragile* from *P. lucius*. Specimens of *Ophiotaenia* reported from *P. lucius* in the present study appear distinctive and warrant specific status.

MATERIALS AND METHODS

During October 1979, we participated with personnel of the U.S. National Fish Hatchery at Willow Beach, Arizona, in recovering tapeworms that were purged by deworming from some adult squawfish maintained at the hatchery. Isolated portions of the raceways containing the treated hosts were observed over a three-day period and voided worms collected hourly. Tapeworms collected were rinsed in Ringer's solution, lightly compressed between glass plates and fixed with AFA. Specimens were taken to our laboratory at Arizona State University for treatment and study. Subsequently (April 1980), Mr. Roger Hammond of the Willow Beach Hatchery treated additional adult squawfish, collected the voided cestodes, and, after rinsing and fixing as outlined above, provided us with the specimens. In the October 1980 deworming procedure, the anti-

helminthic used was Di-N-butyl Tin Oxide in graded dosages of 480 mg, 960 mg, and 1120 mg per fish per day. In the April 1980 treatment, the hosts were treated once with oxytetracycline HCl (Terramycin) at a rate of 25 mg/pound of fish body weight, with no anti-helminthic drug used.

Specimens were stained with Grenacher's alcoholic borax carmine, Semichon's acetic carmine, and Harris's hematoxylin, using procedures of Meyer and Olsen (1975). Nineteen worms were collected and studied.

RESULT AND DISCUSSION

Tapeworms recovered from squawfish were identified as *Ophiotaenia*, using the keys of Schmidt (1970). Most species in this genus have been reported from amphibian and reptilian hosts with two exceptions from piscine hosts: *O. fragile* (Essex, 1929) (*Crepidobothrium fragile* Essex, 1929) from *Ictalurus punctatus* (Channel Catfish), and *O. synodontis* Woodland 1925 from a siluroid fish, *Synodontis schall*. Freze (1965) proposed that members of the genus *Ophiotaenia* be restricted to species from amphibian and reptilian hosts and that *O. fragile* and *O. synodontis* be assigned to the genus *Proteocephalus* since he felt that the generic characteristic of *testes in two lateral fields* of other authors may be inconsistent. He felt that the generic characteristic of *preformation of the uterus* for amphibian and reptilian members of *Ophiotaenia* sp. of other authors was "unclear." Because of ambiguity regarding embryological devel-

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opment of the uterus as well as position of the preformed uterus, we, along with many others, reject this generic characterization of *Ophiotaenia*. The generic criterion of development and of the *testes in two lateral fields* for *Ophiotaenia*, as used by Wardle and McLeod (1952), Yamaguti (1959), Wardle et al. (1974), and Schmidt (1970), seems more logical than defining a genus by host taxon (fish and amphibian hosts share a common habitat in part).

Ophiotaenia recovered from *P. lucius* resemble *O. fragile* more closely than other described species of *Ophiotaenia*, although there are striking differences; these are summarized in Table 1.

Ophiotaenia critica, n. sp.

HOLOTYPE: UNSM 00000, from *Pteichocheilus lucius*, Willow Beach U.S. National Hatchery, Mohave Co., Arizona; April 1980; collected by Roger Hammond.

PARATYPES: USNM 00000, data as holotype.

DIAGNOSIS: (1) Medium size tapeworm, up to 360 mm by 0.4 to 2.02 mm; (2) rounded scolex without apical organ; (3) proglottids typically wider than long; (4) testes 80 to 270 in number situated in two lateral fields; (5) cirrus sac occupying from 1/7 to 1/4 of proglottid width; (6) short cirrus, 0.08 to 0.21 mm long; (7) genital pore not situated on a papilla; (8) vagina always anterior to and never crossing cirrus sac; (9) no vaginal sphincter; (10) five to nine uterine pouches

unilaterally, usually reaching vitelline bands; (11) parasite of fish.

DESCRIPTION (based on 19 specimens): the Strobila is up to 360 mm long with a maximum width of 2.02 mm. The scolex measures 0.7 to 1.1 mm long and 0.79 to 1.69 mm wide. It is rounded but with a slightly pointed apex (Fig. 1). There are four antero-laterally directed, rounded suckers, 0.32 to 0.61 mm in diameter. The apical sucker is absent. The neck is 7.42 to 13.68 mm long, 0.32 to 1.44 mm wide. It is narrower than the scolex anteriorly (Fig. 1). Most proglottids are broader than long.

There are 80 to 270 testes, 0.02 to 0.4 mm in diameter, in two lateral fields. The vas deferens is straight extrabursally in young proglottids; coiled intra- and extrabursally in older ones (Fig. 2). In gravid proglottids the coils form a medullary mass up to 0.5 mm long. The cirrus sac is 0.20 to 0.35 mm long, 0.07 to 0.11 mm wide, occupying from 1/7 to 1/4 of proglottid width. The cirrus is short, 0.08 to 0.21 mm long.

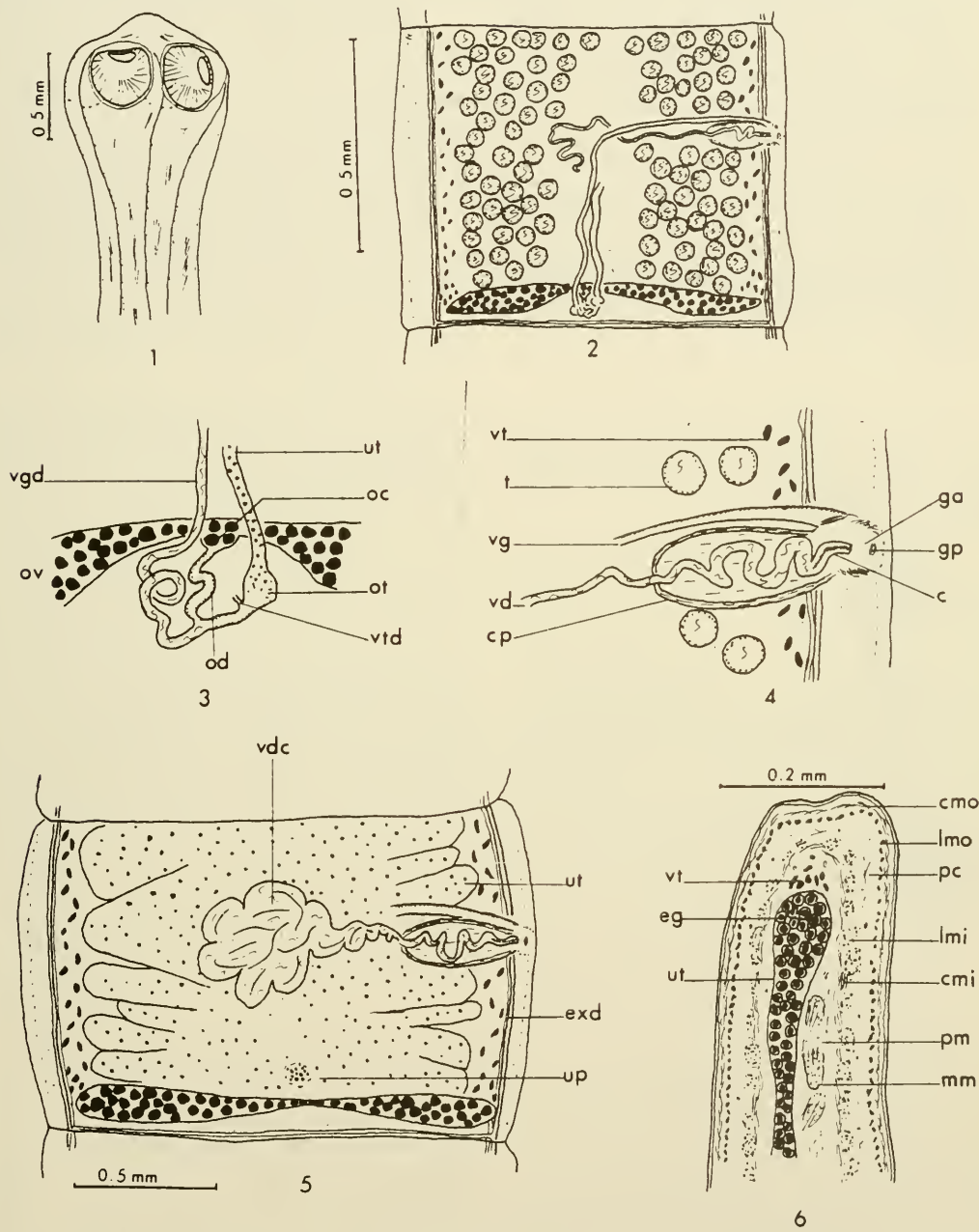
The genital pore is at either the left or right lateral margin of each segment, anterior to median transverse axis. No genital papilla is present.

There are two lateral bands of follicular vitellaria slightly more massive posteriorly. The ovarian lobes are slender and more pointed laterally in younger proglottids. The vagina is anterior to the cirrus sac and never crosses the latter. There is no vaginal sphincter (Fig. 4). The organs of the interovarian space are as in most proteocephalata (Fig. 3).

TABLE 1. Comparison of *Ophiotaenia critica* with *O. fragile*, the most similar congener.

Character	<i>O. fragile</i>	<i>O. critica</i>
Eversion of cirrus	high frequency	no tendency
Length of cirrus	0.88-1.24 mm	0.08-0.21 mm
Vagina	anterior or posterior to cirrus sac	anterior to cirrus sac
Vaginal sphincter	well developed	absent
Scolex	0.5-0.5 mm	0.7-1.1/0.7-1.7 mm
Total strobila length	45-80 mm	up to 360 mm
Fragility	high	normal
Uterine pouches	7-12 pairs	5-9 pairs
Number of testes	150-230	80-270
Diameter of testes	0.07-0.09 mm	0.02-0.04 mm
Uterine pouches	fall short of vitallaria (testes between vitellaria and uterine pouches)	reach vitellaria (testes usually disappear)
Diameter of onchosphere	0.013-0.016 mm	0.017-0.021 mm
Cirrus sac size	0.16-0.19/0.30-0.35 mm	0.20-0.35/0.07-0.11 mm

The uterus has 5 to 9 pairs of lateral proglottids and the testes then disappear. There are one to three uterine pores in the central area of each segment. The



Figs. 1-6. *Ophiotaenia critica*: 1, scolex and portion of neck; 2, mature proglottid; 3, female reproductive organs; 4, reproductive system; area of gonopore; 5, gravid proglottid; 6, transversal section through a gravid proglottid (half represented). Abbreviations: c, cirrus; cmo, outer circular musculature; cmi, inner circular musculature; cp, cirrus pouch; eg, eggs; exd, excretory duct; ga, genital atrium; gp, genital pore; lmo, outer longitudinal musculature; lmi, inner longitudinal musculature; mm, medullary musculature; oc, oocapt; od, oviduct; ot, ootype; ov, ovary; pc, cortical parenchyma; pm, medullary parenchyma; t, testes; up, uterine pore; ut, uterus; vd, vas deferens; vdc, coils of vas deferens; vg, vagina; vgd, vaginal duct; vt, vittellaria; vtd, vitteline duct.

onchospheres are 0.017 to 0.021 mm in diameter.

The reproductive organs are in the medullary parenchyma (Fig. 6).

ETYMOLOGY: The specific name is derived from the latin *criticus*, meaning critical, or decisive, and is used in reference to the endangered status of the host.

ACKNOWLEDGMENTS

We are grateful to Drs. E. Bertke, W. Minckley, and D. Rasmussen, and especially to Dr. M. Fouquette of the Arizona State University Zoology Department for their helpful comments on earlier drafts of this paper.

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SUMMER FOOD HABITS OF COYOTES IN CENTRAL WYOMING

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ABSTRACT.— Summer food habits of coyotes (*Canis latrans*) were investigated on a 3100-km² area in central Wyoming, divided into one deer-use area and five non-deer areas. Analysis of 404 scats (fecal samples) revealed an overall average of 63 percent occurrence of native ungulates, 63 percent leporids, 46 percent rodents, 14 percent livestock, and 11 percent birds. Pronghorn (*Antilocapra americana*) was the ungulate most frequently consumed, occurring in about 87 percent of the scats. Mule deer (*Odocoileus hemionus*) occurred in only 8 percent, and in 5 percent the native ungulate remains were not identifiable beyond order. This large percentage of big game in the diet is apparently unusual, because big game has been of minor importance in most coyote food-habit studies. The high incidence of leporids is consistent with other studies performed in arid intermountain areas. Although cricetines, especially deer mice (*Peromyscus maniculatus*), were trapped consistently in all habitats, months, and trapping areas, they were found in scats at a lower frequency than microtines and sciurids. This suggests a coyote hunting strategy that selected for the latter two groups.

This study was done by the Wyoming Game and Fish Department to determine the summer food habits of coyotes (*Canis latrans*) in central Wyoming. This project was conducted from June through September 1977, and was one aspect of a general study of ecological relationships between mule deer (*Odocoileus hemionus*) and coyotes (Springer and Wenger 1981).

The study area encompassed about 3100 km² in central Wyoming. The southwest corner was about 26 km north of Rawlins (Fig. 1). The North Platte River and two reservoirs formed the eastern boundary, and the area was centrally bisected by the Ferris and Seminole Mountains. Elevation varied from 2000 to 3077 m. Long term mean maximum and minimum temperatures for June–September are 26.2 and 9.2 C, respectively (Becker and Alyea 1964a). Mean total precipitation for June–September is only 2.3 cm (Becker and Alyea 1964b).

Approximately 80 percent of the study area is federally owned, and administered by the U.S. Bureau of Land Management, U.S. Fish and Wildlife Service, and U.S. Water and Power Resources Service. About 10 percent of the land is state owned, and 10 percent privately owned. Prior to and during this study, the land was managed as

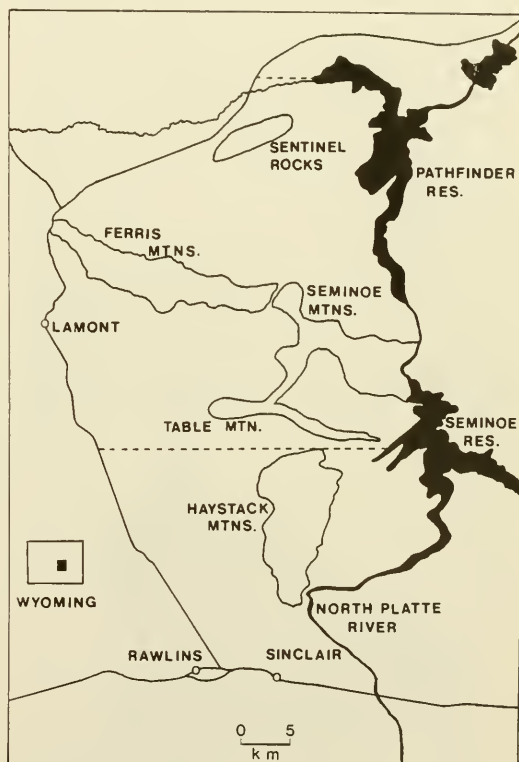


Fig. 1. Study area in central Wyoming, showing the boundaries and major topographic features.

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rangeland, with ranchers specializing in cattle and some sheep.

MATERIAL AND METHODS

Scat Collection and Analysis

Because coyotes do not defecate in a random manner, ground searches for areas of fecal deposition were conducted throughout the study area each month. Areas where coyote scats (feces) were commonly located were fence lines, exposed ridges, dry creek beds, roads, cattle trails, and game trails. Coyote pup scats were also collected at den sites.

The study area was subdivided into six collection sites based on vegetative and geographic difference (Fig. 2). Area I had an abundance of grasses and shrubs seldom taller than 0.3 m and had many creeks and dry washes running between the Ferris and Seminole Mountains and Pathfinder Reservoir. Area II had similar vegetation, but generally flat topography. Area III had vegetation similar to Areas I and II, but had rolling terrain. Area IV was relatively flat and dominated by sagebrush (*Artemisia* spp.) regularly taller than 0.5 m. This area lay almost entirely within the Great Divide Basin, where precipitation runoff never reaches a drainage connected to an ocean. Area V has vegetation similar to Area III, but had many creeks flowing through it, running between the Seminole Mountains and Seminole Reservoir.

Area VI included all mountains, rocky hills and ridges, a pocket of potholes near the center of the study area, and a 2-km strip along a creek that emptied into Pathfinder Reservoir. Vegetation in Area VI was dominated by shrubs taller than 0.5 m, with some above 1.0 m, willow (*Salix* spp.) stands, aspen (*Populus tremuloides*) groves, fir (*Abies* spp.), juniper (*Juniperus* spp.) and pine (*Pinus* spp.).

Each scat was tagged with the date and collection site, placed in a paper bag, and stored for later analysis. Individual scats were securely tied within nylon bags and washed in a low-suds solution in a normal top-loading washing machine. All samples were washed for 4 cycles and broken up by hand between cycles. Washing broke up the fecal matrix, removing all soluble material, and facilitated separation of each scat into various subsamples. Washed scats were tumble-dried at medium heat for an hour until thoroughly dry.

Identification of hair medullas followed the procedure of Moore et al. (1974). Scale casts were made by using the technique described by Johnson (1978). A hair reference collection maintained by the Wyoming Game and Fish Research Laboratory was available for comparison with samples, as were mammal specimens in the University of Wyoming Vertebrate Museum.

Chi-square tests were performed and levels of significance are given where appropriate. An approximate 95 percent confidence interval on a proportion is given by the value:

$$p \pm Z_{0.05} \frac{p(1-p)}{\sqrt{n}},$$

where p is the percentage of occurrence, $Z_{0.05}$ denotes the 5 percent "two-tailed" Z value from a standard normal distribution, and n is the number of scats analyzed (Mendenhall 1975, p. 403). Because

$$p(1-p) \leq 0.25,$$

a conservative 95 percent confidence interval (C.I.) is given by

$$\pm 2 \frac{.25}{n},$$

which simplifies to

$$\pm \frac{1}{\sqrt{n}},$$

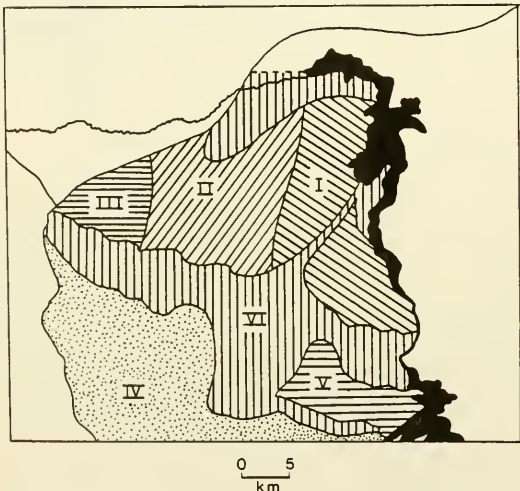


Fig. 2. Six areas within the study area from which coyote scats were collected. Note that Area VI has a northern portion separated from the main part.

Small Mammal Trapping and Rabbit Census

Small mammal species diversity and abundance were determined by trapping. The large size of the study area required a sampling scheme that could solve problems of economics and logistics. Roadways at least 16 km long that passed through a variety of habitat types were used for trapping transects. At intervals of 1.6 km on alternate sides of the road, a live-trap grid or a snap-trap line was laid out adjacent to the road with a maximum of two live-trap grids/transects. (For example, km 1.6 might have a live-trap grid in sagebrush, km 3.2 a snap-trap line in sagebrush, km 4.8 a snap-trap line in grassland, km 6.4 a snap-trap line in wet meadow, km 8.0 a live-trap in mixed browse, etc.)

The snap-trap lines were composed of 10 stations spaced 10 m apart, with two Museum Special traps or Victor rat traps/stations. The live-trap grids were usually in a seven-by-seven station arrangement, but varied in some instances because of the topography. The stations were spaced 15 m apart with two Sherman live-traps/stations. The live-trap grids were run for four consecutive nights, and the snap-trap lines were run for three consecutive nights. Each morning all traps were checked, reset, and rebaited with a mixture of rolled oats and peanut butter.

Spotlight censuses were used to determine the relative abundance of leporids on the study area. Each month, four census routes were driven. A 200,000 candle-power vehicle-mounted spotlight was used to search approximately 10 m on both sides of the road while driving between 25 and 35 km/hour. Spotlight censuses were started at least 30 minutes after dark and continued for about three hours.

RESULTS AND DISCUSSION

In total, 404 scats were analyzed and tabulated (Table 1). Results for the whole study area by month are shown in Table 2. Total results from each of the six collection areas (Fig. 2) are shown in Table 3. Area VI (Fig. 2) was considered to be the deer-use area, and results from Area VI were compared to the combined results of all other areas (Table

3). To determine if the soil and vegetational differences between the north and south sides of the mountains had any significant effect on coyote diet, results from the north areas (I, II, III) were compared to the south areas (IV, V), shown in Table 3.

NATIVE UNGULATES.— Pronghorn, mule deer, and elk (*Cervus canadensis*) were the three most abundant native ungulates that inhabited the study area, though white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*) were present in small numbers. No scats were collected from elk summer habitat; thus all occurrences of cervid hair in the scat samples were presumed to be from mule deer.

Considering the entire study area, native ungulates equaled leporids as the most important food group, on the basis of percent

TABLE 1. Analysis of 404 coyote scats collected from the entire study area. Values are percentages of all scats. An approximate 95 percent confidence interval for this table is ± 5 percent of the values given.

FOOD ITEM	PERCENT	
	Species	Group
Leporids (<i>Lepus townsendii</i> , <i>Sylvilagus audobonii</i>)		63
Pronghorn Antelope (<i>Antilocapra americana</i>)	55	
Mule Deer (<i>Odocoileus hemionus</i>)	5	
Unidentifiable native ungulate	3	
Total native ungulates		63
Sciurids (<i>Spermophilus richardsonii</i> , <i>S. tridecemlineatus</i> , <i>Eutamias minimus</i>)	21	
Microtines (<i>Microtus spp.</i> , <i>Lagurus curtatus</i> , <i>Phenacomys intermedius</i> , <i>Clethrionomys gapperi</i>)	13	
Unidentifiable Cricetidae	7	
Cricetines (<i>Peromyscus maniculatus</i> , <i>Onychomys leucogaster</i>)	3	
Western Jumping Mouse (<i>Zapus princeps</i>)	1	
Northern Pocket Gopher (<i>Thomomys talpoides</i>)	Tr	
Heteromyids (<i>Dipodomys ordii</i> , <i>Perognathus fasciatus</i>)	Tr	
Total rodents		45
Unidentified plant material		42
Coyote (<i>Canis latrans</i>)		22
Arthropods (Coleoptera and Orthoptera)		18

occurrence, both with a 63 percent (± 5 percent) occurrence. Logically, a single occurrence of an ungulate should represent more calories consumed than a single occurrence of a leporid. Native ungulates had the highest percent occurrence for every month but August (Table 2), though only significantly higher in June ($P < .05$), in the deer (Area VI), and in Area II (Table 3). In specific collection areas, the occurrence of native ungulates varied from a low of 22 percent (± 16 percent) in Area III up to 80 percent (± 10 percent) in Area VI (deer-use area). Pronghorn was the ungulate most frequently consumed by coyotes as measured by percent occurrence in all months and geographical areas (including the deer-use area). Deer remains were found only in scats collected in the deer-use area (Area VI). On a monthly basis, deer remains were found only in scats collected in June and July, with 14 percent (± 10 percent) and 6 percent (± 16 percent) respective frequencies of the total for native ungulates for those months.

There are few reports of large ungulates having a high frequency of occurrence as coyote food. Ozoga and Harger (1966) reported a 90 percent occurrence of white-tailed deer in coyote scats collected in northern Michigan in winter. Horn (1941) found a 60 percent occurrence of deer in 7000 scats collected year-round in Santa Barbara County, California. Other studies with comparatively large occurrences of native ungulates include Zadra (1977), with a 45.3 percent occurrence in southeastern Wyoming; McLean (1934), with a 41.7 percent occurrence in California; Ogle (1971), with a 41.6 percent occurrence in Washington; and Hawthorne (1972), with a 35.2 percent occurrence in Sagehen Creek Basin, California.

The high frequency of occurrence of ungulate remains in coyote scats in this study was likely related to availability of ungulate prey. Pronghorn were abundant throughout the study area at lower elevations, and deer occurred in high numbers in the deer-use area. This high availability of native ungulates undoubtedly contributed to the coyote summer diet through direct predation on fawns and perhaps on adults, and by consumption of carrion. It is well documented that coyotes prey on adult and fawn pronghorn (Thompson 1949, Arrington and Edwards 1951, Udy 1953, and Beale and Smith 1973) and deer (Alton 1938, Horn 1941, Cahalane 1947, Robinson 1952, Cook et al. 1971, Hawthorne 1972, and Salwasser 1974). Carrion was available from diseased individuals, road kills, birth complications, and postpartum fawn mortality. Carrion resulting from hunter cripple losses and winter mortality would not have been detected during this study. The frequency data show that coyotes utilized big game as a major food source here. Remains of pronghorn or deer occurred consistently in scats collected in all four months, geographic locations, and collection sites. The extent to which coyotes acted as predators or scavengers could not be deduced from this study.

LEPORIDS.— White-tailed jackrabbits (*Lepus townsendii*) and desert cottontails (*Sylvilagus audubonii*) were placed in this broad category because of the difficulty in differentiating leporid hair. These species and native ungulates had the highest frequency of occurrence in scats over the entire study area. Leporids occurred most frequently in scats obtained in August, though they were not significantly higher than the

TABLE 2. Major food groups found in coyote scats collected throughout the summer expressed as percentage of all scats. Does not include 90 scats collected at 2 den sites.

FOOD GROUP	June	July	MONTH	September	Total ¹
	(N = 104)	(N = 137)	August (N = 33)	(N = 40)	(N = 314)
Native ungulate	64	73	61	73	69
Leporid	48	66	76	68	61
Rodent	37	43	45	43	41
Livestock	12	14	6	8	12
Bird	11	10	24	25	14
Approximate 95% C.I. ²	($\pm 10\%$)	($\pm 9\%$)	($\pm 17\%$)	($\pm 16\%$)	($\pm 6\%$)

¹Weighted average.
²The C.I. is a percentage of the values given.

frequency of native ungulates ($P > .05$). Leporids were significantly ($P < .01$) the most important food item in the north, south, and Areas I, III, and IV. Leporids predominate as a staple in the coyote diet in studies performed on the plains and arid intermountain areas similar to this study site (Sperry 1933, 1934, 1939, 1941, Murrie 1945, Fichter et al. 1955, Fitch and Packard 1955, Tiemeier 1955, Clark 1972, Mathwig 1973).

During the spotlight census, a total of 167 leporids was seen in 361 km driven, for an index of 0.46 animals/km. This number is low compared to similar data collected on this area during previous years. There was no significant correlation ($r = .27$) between the number seen per area and the frequency of occurrence of leporid remains in scats analyzed. The discrepancy between the high frequency in scats and relatively low population index could be due primarily to two factors. The census technique could have biased the numbers seen, and significantly more cottontails and jackrabbits might have been present in rocky and dense vegetation areas that could not be censused. The second possibility is that coyotes on the study area could have been highly selective for leporids in their hunting behavior.

RODENTS.—Rodents occur in nearly all food habit studies of coyotes and usually rank in the top three most important food items. They are usually found to be most important in studies performed in mountainous, coastal, and more mesic areas (O. J. Murie 1935, A. Murie 1940, Ferral et al. 1953, Wilson 1967).

In this study all rodents taken as a group were third in frequency of occurrence, appearing in 46 percent (± 5 percent) of the scats over the entire study area. Occurrence of rodents in the north (47 percent) was significantly greater ($P < .05$) than occurrence in the south (35 percent).

Some taxa can never be reliable distinguished from each other by hairs or bone fragments, and other taxa can only be distinguished from each other when hairs and skeletal parts occur together in a sample (Johnson 1978). Rodents were placed in the major groups shown in Table 1. For comparison, all rodents were placed into two main groups: mice and rats, and sciurids. Compared to sciurids, mice and rats were more utilized

over the entire area ($P < .05$) and in Areas I ($P < .05$), II, III, and IV ($P < .01$). In every area and collection site, microtines occurred most frequently. Cricetines, geomyids, heteromyids, and zapodids occurred only rarely. Sciurids were more important in Area V ($P < .01$), with 69 percent (± 14 percent). This site was adjacent to a prairie dog town, however, in which 67 percent of the 69 percent was found to be *Cynomys*.

In our attempt to determine which species of rodents were available to coyotes, we found deer mice were the only species that appeared consistently in all habitats, months, trapping grids, and trapping transects. Yet deer mice occurred in less than 3 percent of the scats analyzed. Microtines, which occurred most frequently (13 percent), never appeared in the trapping grids or trapping transects. Sciurids, which were important food items, were rarely trapped.

Habitat affinities for cricetids, heteromyids, and sciurids were determined by Maxwell (1967) in eastern Wyoming. The same basic habitats were sampled in this study area, yet fewer species were caught. By using both live-traps and snap-traps, bias in the form of a proneness for a species to approach or avoid a trap should have been removed. There are several factors that probably affected trapping success. The size of the study area precluded intensive trapping efforts in each habitat. This reduced the chances of capturing the rare or elusive species. With such a large study area, logistics and economics played a larger role in planning and implementing the trapping scheme. Some of the species that presumably inhabited the study area (Long 1965) occurred in higher elevations (which were not sampled) or in very limited riparian habitat. Runways for trap placement to increase the trapping success of certain sciurids and microtines were not actively sought. Also, rodent numbers (except *Peromyscus*) could have been low, and the occurrence of voles and squirrels in scats might have been due to selective feeding by coyotes. Another factor could be that *Peromyscus* do not use runways and are more nocturnal, which would make them more difficult for coyotes to catch. Laying down a grid and checking it for several consecutive days could alter the trapability of certain

rodents (Manville 1949, Kikkowa 1964, and Sheppe 1967). Finally, trapping as a method of determining population characteristics may not be completely valid. The determination of home ranges by trapping methods has been criticized by Hayne (1950); it reveals the complex relationship between an animal and a set of traps rather than a biological characteristic of the animal's normal life history.

LIVESTOCK.—Livestock were grazed on more than 90 percent of the study area but only occurred in 14 percent (± 5 percent) of all scats analyzed. Cattle accounted for 8 percent (± 5 percent) and sheep 6 percent (± 5 percent) of the livestock occurrences. Compared to sheep, cattle occurred more frequently in all months in Areas I, II, III, and IV, though sheep occurred more frequently than cattle in Area IV.

Sperry (1941) felt that most body parts of livestock found in coyote diet samples were from carrion. This also has been suggested by others (Fichter et al. 1955, Gier 1968, Clark 1972, and Meinzer et al. 1975). Klebenow and McAdoo (1976), however, found the coyote to be a major predator on sheep in northeast Nevada, as did Dorrance and Roy (1976) in Alberta. A few cases of clear coyote predation were observed, and predation on sheep was reported to be a problem by one ranch on the study area. Animals that were found dead of other causes were not observed to be fed upon during the course of the coyote food habits study.

BIRDS.—All birds are lumped into one group because only shafts of feathers were

recovered, and no positive identification could be made. Bird remains were found in 11 percent (± 5 percent) of the scats collected over the entire study area. Occurrences of birds were highest in September (25 percent ± 16 percent), and in Area I (27 percent ± 15 percent). Sage grouse (*Centrocercus urophasianus*) were available throughout the study area and may have been the main contribution to the bird remains.

ARTHROPODS.—Beetles (*Coleoptera*) and grasshoppers (*Orthoptera*) were found in 18 percent (± 5 percent) of the scats but mostly in trace amounts. Only two scats were found to be made up almost exclusively of grasshoppers.

VEGETATION.—Plant fragments were found in 45 percent (± 5 percent) of all scats. Almost all samples contained only a trace of vegetation. It is felt that most vegetation in scats resulted from incidental consumption during normal feeding and the adherence of leaves and twigs to feces after defecation.

REPTILES.—Unidentified snake remains were found in four scats.

COYOTE.—Some coyote was found in 20 percent (± 5 percent) of all scats. Most of one scat was composed of coyote hair, indicating a possible instance of cannibalism. Trace occurrences in other scats were probably due to grooming by the coyotes.

CONCLUSIONS

This study was done to help determine if coyote predation was a significant depressant

TABLE 3. Major food groups in coyote scats collected in different areas (Fig. 2) throughout the summer, expressed as percentage of all scats containing the group specified.

FOOD GROUP	AREA						Non-deer ²	North ³	South ⁴	Total ⁵
	I (N = 45)	II (N = 86)	III (N = 37)	IV (N = 101)	V (N = 54)	VI ¹ (N = 81)				
Native ungulate	62	78	22	52	63	80	59	62	56	63
Leporid	78	72	70	62	63	42	68	69	67	63
Rodent	42	42	27	31	69	63	41	47	35	45
Livestock	4	8	35	13	0	17	11	12	10	12
Bird	27	15	3	8	6	12	12	10	14	11
Approximate 95% C.I. ⁶	$\pm 15\%$	$\pm 11\%$	$\pm 16\%$	$\pm 10\%$	$\pm 14\%$	$\pm 11\%$	$\pm 6\%$	$\pm 8\%$	$\pm 8\%$	$\pm 5\%$

¹Area VI was the only high deer-use area.
²Non-deer areas were Areas I, II, III, IV, and V.
³North was Areas I, II, and III; scats from dens not included.
⁴South was Areas IV and V; scats from dens not included.
⁵Weighted average for the entire study area.
⁶The C.I. is a percentage of the values given, not a percentage of N.

to mule deer populations. Coyotes on this study area consumed mule deer, either through predation or as carrion, as shown by scat analysis. Pronghorn occurred more frequently in scats because of their wider distribution. There was a conflict in this study area between man (his interest in ungulates as game and livestock) and coyotes (their interest in ungulates as food). Food habits studies cannot resolve this conflict. More information is needed: population sizes of coyotes and potential prey, hunting pressure by man, predation rates, productivity rates of coyotes and prey species, availability of carrion, effects of predator control, and other important parameters. Several of these areas were investigated and reported by Springer and Wenger (1981). Food habits studies can, however, indicate to wildlife managers that a potential problem exists. The fact that native ungulates occurred so frequently in the coyotes' diet certainly indicates that a problem could develop if coyote numbers become higher.

ACKNOWLEDGMENTS

We thank M. S. Boyce, D. Crowe, W. G. Hepworth, L. L. McDonald, J. E. Prairie, E. C. Springer, and C. R. Wenger for help in the field and laboratory and with manuscript preparation. Special gratitude is due to T. D. Moore for his invaluable and patient aid during the scat analysis. Data presented here were included in a thesis by Smith (1979).

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MICROENVIRONMENT AND NEST SITE SELECTION BY RING-NECKED PHEASANTS IN UTAH

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ABSTRACT.—Vegetative and atmospheric parameters were evaluated at 16 different nest sites of ring-necked pheasants in Utah County, Utah, to determine which parameters are influential in the nest site selection process. These data indicate that total vegetative ground cover, high amounts of cover immediately surrounding the nest cavity, and drying power of the air are the parameters most influential in nest site selection.

Several aspects of the environment have been reported to influence nest site selection by ring-necked pheasant hens. Hammerstrom (1936) proposed that pheasant nests occur more often around the periphery of fields. Nelson et al. (1960) evaluated several previously published studies, however, and found that nest densities near the edge of the field were equivalent to densities in the interior of the fields.

The importance of vegetative structure on pheasant nest placement has been the subject of several investigations. Hanson (1970) implicated the importance of vegetative cover and height on pheasant nest site selection within cultivated hay fields. The influence of vegetative canopy over the nest site was evaluated by Wagner et al. (1965). Salinger (1952), Bartmann (1969), and Baxter and Wolfe (1973), have shown that pheasants prefer to nest in residual cover from the previous season's growth or among early-growing plant species. One early-growing plant species abundant in most pheasant ranges is alfalfa. Olsen (1977) summarized 14 studies and found an average of 44 percent of all nests located in alfalfa, though this habitat provided only 21 percent of the total successful nests and 10 percent of the overall chick production. In contrast, wetlands contained 14 percent of the nests but produced 33 percent of the successful nests and 28 percent of the total chick production.

Other researchers have concentrated their efforts on the influences of temperature, humidity, and solar radiation on nest site

selection and nesting success. Graham and Hesterberg (1948) were the first to implicate the effect of climate on ring-necked pheasant distribution. Yeatter (1950) documented the influence of temperature on pheasant populations. Studies on the ability of hen pheasants to select nest sites with optimum temperature and saturation deficit have been conducted by Francis (1968) and by Schulte and Porter (1974).

This study will collectively reevaluate the influence of solar radiation, temperature, saturation deficit, and vegetative structure on the selection of a nest site by ring-necked pheasant hens in central Utah.

METHODS

Nests were located in Utah County, Utah, using a procedure similar to that outlined by Stokes (1954). The procedure consisted of visually searching a portion of each habitat type along 1 m wide transects. This procedure has been tested by Labisky (1968) and Baxter and Wolfe (1973), using dummy nests secretly placed in various cover types, and was found to be approximately 90 percent accurate.

Once nests were located, percent vegetative cover within a $\frac{1}{4}$ m² area surrounding the nest cavity, vegetation height, percent canopy cover immediately above the nest cavity, and percent side cover immediately surrounding nest cavity were recorded. Light intensity, humidity, and temperature within the nest cavity and above the vegetation

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were also recorded. Readings on these atmospheric parameters were repeated at random on subsequent days at several nest sites. All data were collected between 0800 and 1830 hours under varying weather conditions during the month of June 1979.

For each nest site found, an adjacent non-nest site was randomly selected in the same vegetation type. Position of the nonnest site was determined by turning away from the largest area of the habitat that was similar to the nest site and throwing the quadrat used for cover estimation over the shoulder. Identical measurements were then taken on those sites. This allowed paired comparisons of parameters affecting nest and nonnest sites. All data were analyzed for normality of distribution using a mean-to-variance ratio equal to one as the standard for the test. Vegetation height, percent canopy cover, percent side cover, and light intensity were not normally distributed ($p < 0.05$). Data collected on these parameters were evaluated using appropriate nonparametric techniques (Gibbons 1976).

TABLE 1. Summary of habitat types in which nest sites were located. The table also includes the predominant plant species and the number of observations recorded at each nest site.

Habitat	Major plant spp. at nest site*	Number of nests	Number of observations at each nest
Hayfield	alfalfa	4	1,2,2,6
	smooth brome	1	2
Irrigated pasture	tall wheatgrass	3	2,5,6
Wet meadow	sedges	1	3
	wiregrass	1	2
Herbaceous weeds	whitetop	2	1,3
	pepperweed	1	3
Woody shrubs	saltcedar	1	1
	greasewood	1	4
	big sagebrush	1	1

*Scientific names of plants listed above:
alfalfa *Medicago sativa*
smooth brome *Bromus inermis*
tall wheatgrass *Agropyron elongatum*
sedges *Carex* spp.
wiregrass *Juncus* spp.
whitetop *Cardaria draba*
pepperweed *Lepidium perfoliatum*
saltcedar *Tamarix ramosissima*
greasewood *Sarcobatus vermiculatus*
big sagebrush *Artemisia tridentata*

Percent vegetative cover was determined by ocular estimation, using a ¼ m² quadrat centered on the nest. Determination of percent canopy cover directly above the nest cavity and percent side cover immediately surrounding the nest cavity was also by ocular estimation. Height of vegetation was measured directly with a meter stick. Light intensity within the nest cavity and in the air above the vegetation was measured with a Gossin Luna-Pro light meter. Relative humidity (greater than 25 percent) and temperature were measured within the nest cavity and in the air above the vegetation with a Lufft hygrometer. Saturation deficit was calculated as an index of the drying power of the air as suggested by Francis (1968). Saturation deficit was calculated by finding the appropriate saturation vapor pressure at the measured air temperature (in tables of the Handbook of Physics and Chemistry) and subtracting from that value the actual vapor pressure. Actual vapor pressure was calculated by multiplying saturation vapor pressure by percent relative humidity divided by one hundred.

RESULTS AND DISCUSSION

Data were collected on 16 nests located in five distinct habitat types (Table 1). Data are summarized in Table 2. Percent vegetative cover at the nest site was significantly higher ($p < 0.05$) than that found at the adjacent nonnest sites. Furthermore, comparison of the variance between the two samples showed that nest sites deviated significantly less ($p < 0.05$) from the average percent vegetative cover than did the nonnest sites (Table 3). The percent side cover immediately surrounding the nest cavity also indicated that the hens were sensitive to vegetative structure. Although the median for the nest site did not differ significantly from that of the nonnest site for this parameter, comparison of the distributions of the two sets of data shows a significantly smaller range of values around the median of the nest site ($p < 0.01$).

Vegetative height above the nest cavity showed no significant difference in the medians or in the distributions of data about the medians when comparing the nest and non-nest sites. Vegetative height at the nest site

varied from a low of 40 cm to a high of 271 cm (1.3 to 8.9 feet). Hansen's (1970) data suggest that pheasants may be selecting nest sites with specific vegetative height. Nevertheless, the strongest correlation his data indicated was between an index of average vegetative cover (plant height times plant density) in a given field and nest density in that field.

Data collected on canopy cover indicated that this factor does not influence nest site selection. No differences were noted between the median canopy cover or in the distribution of the recorded values when comparing the nest and nonnest sites. Studies by Wagner et al. (1965) tend to confirm this observation. They reported that, of a total of 502 nests, 30 percent were completely exposed from above, and the exposed nests had equivalent hatching success to unexposed nests.

All atmospheric parameters showed significant differences between values recorded within the nest cavity and values recorded in the air above the vegetation; no differences were found between the nest and nonnest sites when comparing means, medians, or distributions of data sets. Comparison of median light intensities above the vegetation with those recorded within the nest cavity showed that light intensity was greatly reduced. By comparing light intensity within the nest cavity to the intensity in the vegetation of the nonnest sites, however, it was apparent that the hens were not selecting nest sites for some optimum light intensity.

Temperature within the nest cavity was significantly higher than that recorded in the air above the vegetation ($p < 0.005$) by an average of 1.7 C. This is consistent with the results of Francis (1968), who found temperatures significantly higher at 10 cm than at 100 cm above the ground. Comparison of the nest to the nonnest site indicated no ability on the part of the hen pheasants to minimize this increase in temperature. Solar radiation and atmospheric temperature within the nest cavity are the major factors influencing internal egg temperature prior to incubation (Schulte and Porter 1974). Egg temperature in turn influences viability and hatching success (Yeatter 1950). Even so, our data indicate that hen pheasants do not select nest sites that minimize incident solar radiation and temperature effects.

Saturation deficit was found to be significantly lower within the nest cavity than in the air above ($p < 0.05$). The difference in saturation deficit between the nest and non-nest sites was not significant, although a comparison of data between habitats indicated that hen pheasants may be selecting for a minimum saturation deficit. An analysis of variance using deviations from values recorded above the vegetation at the nest and non-nest sites, grouped according to habitat, was conducted on temperature and saturation deficit data. There were no significant differences indicated between habitats for temperature data, or saturation deficit data at the nest site. Saturation deficit data at the non-nest sites, however, indicated a significant difference between habitats ($F_{4,17} = 3.04$ $p < 0.05$). Francis (1968) also reported differences in saturation deficits between habitats. If these differences truly exist between habitats and are not evident at the nest sites, then hens must be selecting environmentally similar areas within different habitats.

By collectively reevaluating several factors that have been previously reported, we have been able to develop a composite picture of factors influencing nest site selection by ring-necked pheasant hens. Ground cover surrounding the nest and drying power of the air

TABLE 2. Mean or median values and sample size for parameters evaluated at the nest site, adjacent site, and in the atmosphere.

Parameter	Sample size	Mean or median value	
		Nest site	Nonnest site
Cover (%) ¹	16	85.6	74.4
Vegetation height ² (centimeters)	16	65	60
Canopy cover (%) ²	16	40	25
Side cover (%) ²	16	85	75
Light intensity ² (foot candles)	44		
Above vegetation		6982	6982
Nest level		623	669
Temperature ¹ (C)	44		
Above vegetation		27.9	28.0
Nest level		29.6	29.4
Saturation deficit ¹ (millibars)	22		
Above vegetation		16.2	16.0
Nest level		15.0	14.3

¹Values recorded are means

²Values recorded are medians

TABLE 3. Results of statistical tests evaluating differences between the nest site, the adjacent site, and the atmosphere. Tabular values represent the maximum probability of rejecting a true null hypothesis.

Parameter	Comparison of nest site to:		Comparison of data distributions between nest and nonnest sites
	Atmosphere	Nonnest site	
Cover (%)	-----	0.050 ¹	0.025 ⁴
Vegetation height	-----	0.402 ²	0.160 ⁵
Canopy cover (%)	-----	0.402 ²	0.352 ⁵
Side cover (%)	-----	0.227 ²	0.012 ⁵
Light intensity	0.0002 ²	0.652 ²	0.367 ⁵
Temperature	0.005 ³	0.270 ³	0.346 ⁵
Saturation deficit	0.055 ³	0.092 ³	0.194 ⁴

¹t-test with unequal variance
²sign test
³paired t-test
⁴F-test for equality of variance
⁵Siegal-Tukey test for equality of distribution

are two factors which seem to be most influential on nest placement. Other factors may be influencing nest placement indirectly by affecting these two factors or their interaction.

ACKNOWLEDGEMENTS

This work was conducted in conjunction with the Utah Division of Wildlife Resources, which was under contract with the U.S. Bureau of Reclamation to conduct a wildlife inventory around Utah Lake for the Central Utah Water Project. We wish to thank Karl Hirst, Miles Moretti, Wes Shields, and Jim Thomas for their help in locating nests.

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BALD EAGLE WINTER SURVEY IN THE SNAKE RIVER CANYON, WYOMING

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ABSTRACT.— A 5-year winter bald eagle survey was conducted along 22 km of the Snake River Canyon in northwestern Wyoming. Surveys were done on 94 days requiring 1,414 hrs and 1,888 km driving. In all, 220 (85 percent adults) bald eagles were seen. Seventy-seven percent of all eagles were perching, 15 percent were flying, 4 percent were feeding on road-killed mule deer, and 4 percent were flying low over water. Perching sites were identified as 32 percent cottonwoods, 30 percent spruce, 17 percent Douglas-fir, and 22 percent other. Eagles were somewhat clumped in distribution.

This paper describes a 5-year winter bald eagle survey along part of the Snake River Canyon in northwestern Wyoming. Data on eagle population size and age structure, temporal and spatial distribution, activities, and perching sites were obtained.

The 22 km canyon study area lies south of Jackson Hole, Wyoming, and begins 6.2 km north of Hoback Junction (highway junction of U.S. 89 and 187) and terminates at a point just north of where the Snake River turns abruptly west (Fig. 1). About 90 percent of the river is observable from the highway that parallels it. Elevations range from 1800 m at the river to 3000 m at the tops of the canyon walls.

The river bottom is dominated by narrow-leaf cottonwoods (*Populus angustifolia*), black cottonwood (*P. trichocarpa*), and whip-lash willows (*Salix lasiondra*). Blue spruce (*Picea pungens*) is intermixed. South-facing canyon walls are dominated by Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and sagebrush (*Artemisia* spp.). North-facing slopes are vegetated by dense stands of Engelmann spruce (*Picea engelmannii*).

Human population is greatest at Hoback Junction and for about 1.6 km on either side. Mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*) winter in and near the canyon.

METHODS

The survey was conducted from an automobile along U.S. Highway 89 beginning in midwinter 1974–1975 and continued at irregular intervals, as time and weather permitted, until late 1979–1980. Frequent stops were made along the route as roads, traffic, and winter conditions allowed. Binoculars were used to scan the river, adjacent trees, and canyon walls for birds at each stop. The canyon was also visually scanned while driving. It required about 1.5 hrs per survey and all raptors were noted. Each survey was conducted generally in late afternoon by a single observer (AHK).

RESULTS

Surveys were done on 94 days over the 5 winters (Table 1) and included 1414 hrs visually scanning and 1888 km driving. Two hundred twenty bald eagle sightings were recorded. Adults ($N=193$) comprised 85 percent of the sightings. In September, one eagle was seen; in October, one; in November, 21; in December, 16; in January, 29; in February, 55; in March, 88; and in April, 9.

The mean number of bald eagles seen per survey was 2.3 (range 1–3). The 1974–1975 winter showed a mean of 2.8 birds per

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survey; 1975-1976, 4.7; 1976-1977, 1.9; 1977-1978, 1.7; and 1980, 3.0. March showed the largest mean number of birds per

survey with 3.1, followed by February with 2.7, December 2.3, January 1.8, November 1.5, April 1.3, and September and October 1.0.

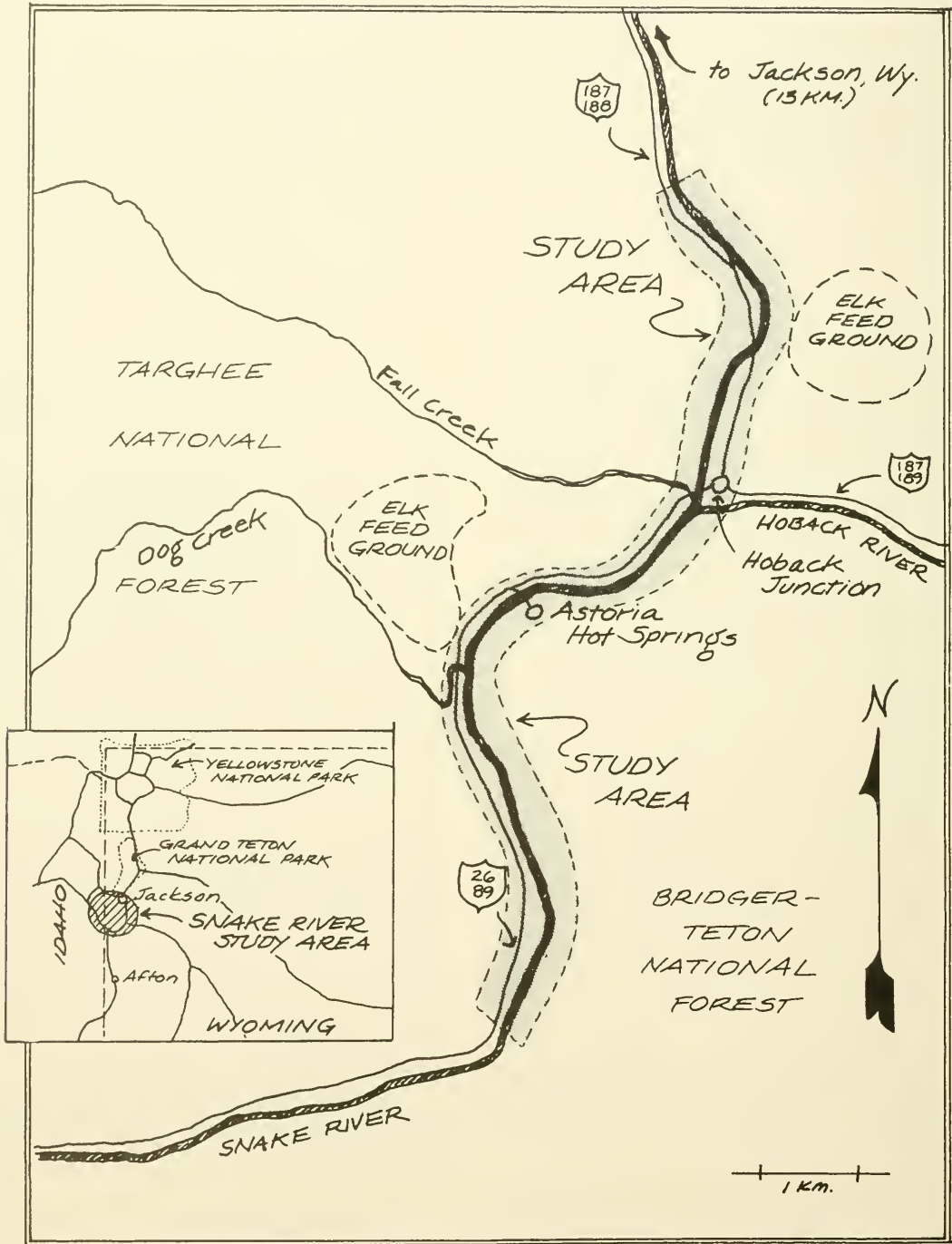


Fig. 1. Location of bald eagle study area in Snake River Canyon, Wyoming (1975-1978, 1980).

Activities were recorded for all 220 birds sighted: 77 percent were perching; about 14.6 percent were flying; 4.4 percent were seen feeding on road-killed mule deer; and 3.9 percent were flying low over water.

The perching site was identified in 169 cases. Fifty-five eagles (32.5 percent) used cottonwoods, 50 (29.6 percent) used spruces, 28 (16.6 percent) used Douglas-fir (old nest site), 19 (11.2 percent) other sites (e.g., ground, rocks), and 17 (10.1 percent) dead snags.

Bald eagles used only the upper one-third of spruce trees for perching (50 in 50 cases), and the middle one-third for cottonwoods (55 in 55 cases), whereas they used the upper two-thirds of snags of both species (17 in 17 cases).

Eagles were clumped in distribution along the 22 km study route. Six concentrations were found. The areas at km 1 and 2, 7, and 13 contained numerous perching sites and the areas at km 16, 20, and 22 all contained one or more active or old nests.

DISCUSSION

The resident winter bald eagle population in the study area is relatively small, probably less than 6 birds. If so, these eagles represent about 20 percent of the greater Jackson Hole population (Davenport and Weaver, in press).

The percent of subadult bald eagles we observed in Wyoming is about half the percentages found in other populations in Utah (Edwards 1969), Montana (McClelland 1973), South Dakota (Steenhof 1976), and in Washington (Stalmaster et al. 1979, Knight et al. 1979). But other areas had as few as 6 percent subadults (Southern 1963, Swenson

1975). Low subadult percentages in Wyoming may reflect low density of carrion as suggested by Stalmaster et al. (1979), which forces subadults to winter further south as suggested by Southern (1964) and Sprunt and Ligas (1966).

Stalmaster and Newman (1979) found that bald eagles in northwestern Washington strongly preferred dead trees for daytime perches. Firs and Douglas-firs were avoided in their study. In South Dakota, Steenhof et al. (1980) found bald eagles preferred mature cottonwoods. We found that bald eagles used the upper two-thirds of cottonwoods and upper one-third of conifers. These perching sites allowed the greatest range of visibility and provided relatively unobstructed flight paths through the crowns as indicated by Stalmaster and Newman (1979), but Steenhof et al. (1980) found proximity of trees to the river and to food more important in habitat selection than tree characteristics.

The clumped distribution of bald eagles along the Snake River was probably due to availability of perching sites and significantly influenced by sites of carrion and fishing areas. Knight et al. (1979) found clumping of eagles in Washington, as did Steenhof et al. (1980) in South Dakota. Stalmaster and Newman (1979) felt that clumping of birds was due to clumping of key habitat elements of diurnal perch sites, proximity to water, feeding sites, nearby open regions, and sighting distances from the perch. Our study did not include measurement of parameters mentioned by Stalmaster and Newman (1979). But from December 1978 to February 1979, 44 dead ungulates provided about 4296 kg of potential food in our study area according to Davenport and Weaver (in press).

TABLE 1. Sampling schedule in days/month by year for the bald eagle winter surveys, Snake River Canyon, Wyoming.

Winters	Months								Total
	S	O	N	D	J	F	M	A	
1974-1975					5	3	7	2	17
1975-1976				2		1	4		7
1976-1977			6	2	2	3	2		15
1977-1978	1	1	8	3	7	1	5		26
1980					2	12	10	5	29
Totals	1	1	14	7	16	20	28	7	94

Because rapidly increasing development and river traffic is occurring in this region of the Snake River Canyon, we suggest that more precise habitat identification is needed and that present habitat structure along shores of the river be maintained as suggested by Stalmaster and Newman (1978).

ACKNOWLEDGMENTS

We thank Denise Casey and Tim Craig for their critical review. Wendy Morgan prepared the study area map.

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LENGTH OF WESTERN TENT CATERPILLAR EGG MASSES AND DIAMETER OF THEIR ASSOCIATED STEMS

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ABSTRACT.—Stems bearing egg masses of the western tent caterpillar (*Malacosoma californicum*), collected in Arizona and northern New Mexico during 1977–1980, had mean diameters between 2.9 and 4 mm. Mean lengths of the egg masses were consistently between 11 and 14 mm.

High populations of the western tent caterpillar, *Malacosoma californicum* (Packard) (Lepidoptera: Lasiocampidae), defoliated substantial areas of trembling aspen, *Populus tremuloides* Michx., in northern New Mexico and southern Colorado in recent years. Larvae were a general nuisance to forest users, not only completely defoliating trees but also causing slick spots on New Mexico highways when cars crushed large numbers of them.

To satisfy inquiries regarding the duration of the infestations, egg masses were collected at various locations to determine population

trends. Although some egg masses were collected on the Kaibab National Forest in Arizona, most were collected from permanent five-tree sample plots on the Sante Fe National Forest in northern New Mexico during 1978–1980. Branches were pruned from lower crowns of trees from 10 to 17 m tall. Egg-mass-bearing twigs were clipped from these branches after the counts were made for population trend predictions and then shipped to Fort Collins, Colorado, where egg mass length and diameter of the associated stem were measured.

TABLE 1. Mean lengths of western tent caterpillar egg masses and diameters of associated stems.

Location ¹	Collection date	Number of egg masses	Length of egg masses (mm)		Stem diameter (mm)	
			\bar{X}	range	\bar{X}	range
Kaibab N.F., Arizona						
Jacob Lake	31 October 1977	44	11.0	8–15		
Santa Fe N.F., New Mexico						
Espanola	25 September–5 October 1978	491	12.3	6–33	3.4	1–14
Tesuque	"	274	13.4	6–29	3.9	1–11
Jemez	"	78	13.6	8–19	3.4	1–8
Coyote	"	92	13.6	9–26	3.4	1–5
Santa Fe N.F., New Mexico						
Espanola	11–24 September 1979	157	12.8	7–18	3.5	1–10
Tesuque	"	29	14.2	9–20	4.0	2–10
Jemez	"	28	13.7	9–17	3.0	2–6
Coyote	"	2	11.0	10–12	3.0	3.0
Santa Fe N.F., New Mexico						
Espanola	20, 28 October 1980	137	12.2	5–18	3.1	1–8
Tesuque	28, 29 October 1980	103	13.4	8–18	2.9	1–6
Jemez	29 October 1980	28	12.8	10–16	3.0	2–4
Coyote	21, 27 October 1980	160	11.8	7–16	3.2	2–8

¹Collections were made on U.S. Forest Service lands near locations shown.

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Tent caterpillar egg masses varied from 6 to 33 mm in length; mean length was consistently between 11 and 14 mm (Table 1), which indicated egg mass length did not change significantly during sample years.

Mean diameter of the associated stem varied from 2.9 to 4 mm (Table 1). The diameters ranged from 1 to 14 mm, but the majority of stems were between 2 and 5 mm. This has practical significance for sampling western tent caterpillar egg masses. Because 96 percent of the egg masses were found on stems 6 mm or smaller in diameter, there is

little need to examine stems of larger diameter. Furthermore, in another study, of the 88 egg masses found on branches throughout the crowns of 12 trees, 93 percent were attached 30 cm or less from the tip of the branchlet. Thus, examination of the stems of branchlets more than 30 cm long will not yield significantly greater numbers of egg masses. If the distribution of egg masses in the crowns of aspen can be determined, then it, plus the stem diameter and distance from the tip, can be integrated to produce a sampling scheme.

UNDERSTORY VEGETATION IN FULLY STOCKED PINYON-JUNIPER STANDS

Richard L. Everett¹ and Susan Koniak¹

ABSTRACT.— Ten fully stocked pinyon-juniper stands contained a total of 73 species in the understory, but the number of understory species in any one stand was moderately low ($\bar{x} = 20$). On each stand, species of at least five different plant groups were present in the understory (shrub, perennial grass, perennial forb, annual grass, or annual forb). A perennial grass, Sandberg bluegrass (*Poa sandbergii*), and a group of annual forbs with relatively high cover and constancy among stands appeared best adapted to coexist with the pinyon-juniper overstory. The proportion of total plant cover was greater on tree-associated microsites (duff and transition) than in the interspace between trees because of the greater surface area of the former in most stands. The transition microsite was the most favorable for understory species and provided understory cover in disproportionately greater amounts than the area it occupied.

In the sampled stands, the majority of available resources was apparently utilized by the tree species (fully stocked), and only a sparse understory existed. Understory species are of little import to total biomass within fully stocked stands of singleleaf pinyon pine (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*), but they represent the only available forage and the species most likely to reclaim the site following disturbance. Numerous small annual forbs and/or scattered suppressed perennial species characterize the sparse understory. A meaningful characterization of the amount and distribution of individual understory species is made difficult by the ephemeral nature of annuals and the patchiness of understory within the stands.

Distribution of understory is not uniform among soil microsites in these woodlands or in other forest situations because of overstory effects on shading, rain interception, and dense duff layers (Anderson et al. 1969). Less visible differences among soil microsites, such as nutrient concentration under the crown and its depletion in interspace zones (Zinke 1962, Barth 1980) and ameliorated microclimate under tree crowns (Johnsen 1962), also effect understory distribution.

The soil surface within fully stocked pinyon-juniper stands can be characterized as a mosaic of duff under the crown, a transition zone of scattered needles surrounding the duff, and bare ground between trees. We

defined duff as a soil microsite with 90 percent or more ground surface covered by needles to a depth greater than 0.5 cm. Transition microsites are defined as having 20–90 percent of the soil surface covered by needles with an average depth of less than 0.5 cm. Interspace microsites are characterized by less than 20 percent needle cover of less than 0.5 cm depth.

It is not the purpose of this study to illuminate characteristics of specific microsites that control understory plant distribution, but to record differences in plant cover between duff and transition microsites and between mean plant cover of these tree-associated microsites and that of interspace. We used the proportion of total plant cover provided by each microsite in a stand and plant cover/m² of each microsite to illuminate these differences.

METHODS

Ten fully stocked stands were sampled for understory species cover and distribution in 1978 (Fig. 1). Observations reflect only a “snapshot” view of the understory vegetation. Subsequent sampling was impossible because trees were soon harvested. At each stand, a square plot 30 m to a side was established. Five line transects 20 m in length were laid out at 5-m intervals parallel to each other across the slope. Tree cover was estimated by line intercept. A 50 × 50 cm

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frame was laid down at every meter mark along the transects, and understory species cover, density, and type of soil microsite were recorded for each frame. Results were

used to estimate plant cover distribution among soil microsites across the entire stand. As sampled microsites along the transect are disjunct and subject to wide variations in

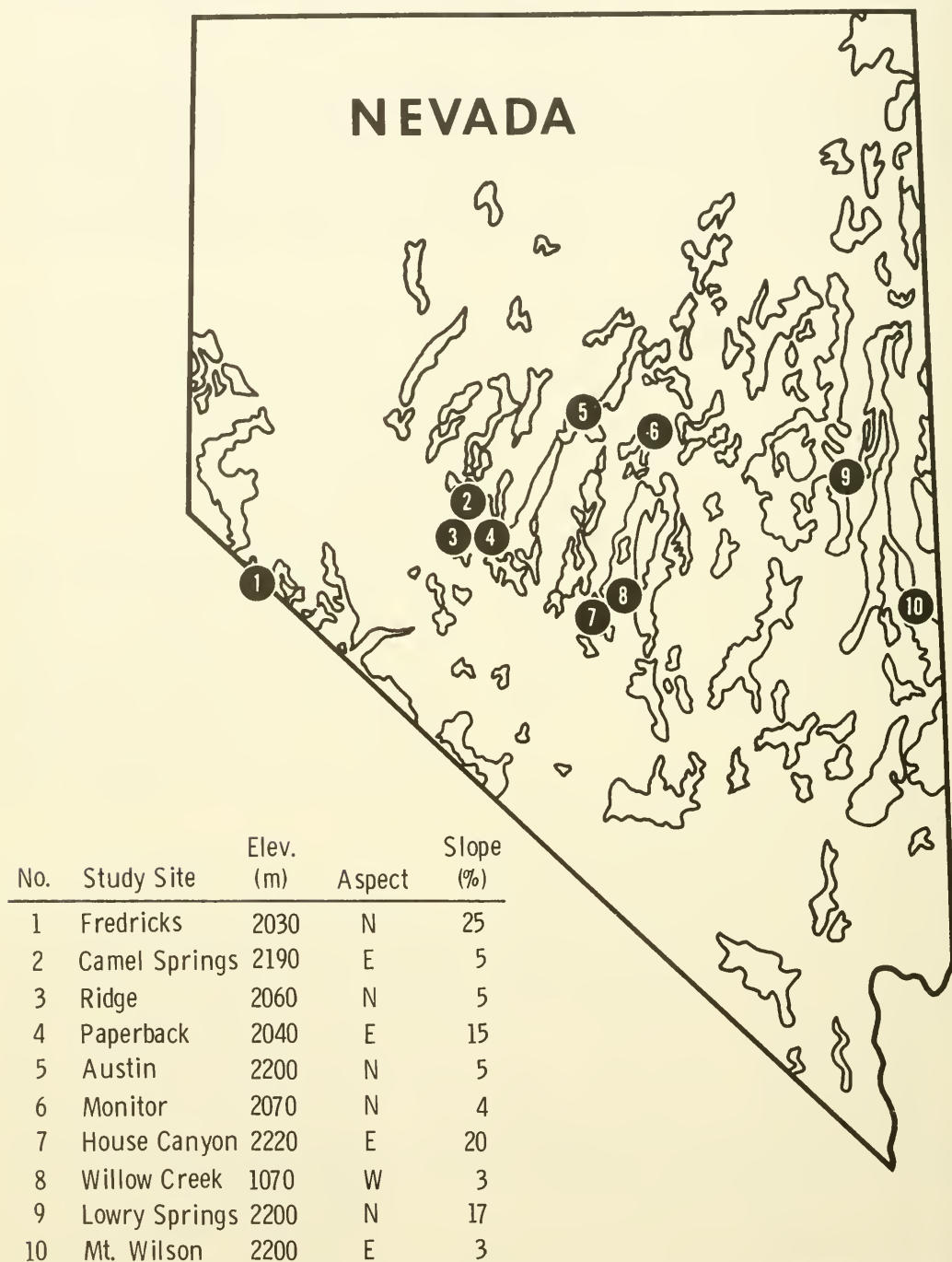


Fig. 1. Location of study sites in relation to pinyon-juniper woodlands of Nevada. Woodland distribution patterns taken from Pinyon-Juniper woodlands of the Great Basin (Tueller et al. 1979).

microclimate, another set of contiguous transects was used to compare differences in plant cover/m² of each microsite.

Four pairs of trees were selected for tree-to-tree transects. Each tree was at least 20 cm in diameter, and trees of each pair had at least 1 m of interspace between them. A series of 50 × 50 cm frames was laid contiguously the entire length of these transects from tree bole to tree bole. It was hoped

contiguous frames reduced microclimate variability among microsites and served to eliminate understory variability due to inclusions of remnants from the past shrub-dominated community. Plant cover and soil microsite type within each frame were recorded. Data were converted to plant cover/m² of each soil microsite, and this was used as a crude estimate of microsite favorableness for understory species.

TABLE 1. Constancy and relative importance values for understory species.

Species ¹	Constancy ²	Relative importance values ³	Species	Constancy	Relative importance values
	percent			percent	
Grass (grasslike)			Shrubs		
<i>Poa sandbergii</i>	90	100.0	<i>Phlox hoodii</i>	80	5.7
<i>Sitanion hystrix</i>	80	5.2	<i>Artemisia tridentata</i>		
<i>Bromus tectorum</i>	40	1.5	spp. <i>caseyana</i>	40	13.3
<i>Stipa thurberiana</i>	20	— ⁴	<i>Purshia tridentata</i>	40	3.5
<i>Agropyron spicatum</i>	10	1.2	<i>Leptodactylon pungens</i>	20	0.2
<i>Carex</i> sp.	10	—	<i>Artemisia arbuscula</i>	10	0.5
<i>Oryzopsis hymenoides</i>	10	0.1	<i>Artemisia tridentata</i>		
<i>Stipa pinetorum</i>	10	0.01	spp. <i>wyomingensis</i>	10	3.3
			<i>Cercocarpus ledifolius</i>	10	—
Perennial forbs			<i>Ephedra viridis</i>	10	0.2
<i>Arabis holboellii</i>	90	1.6	<i>Eriogonum caespitosum</i>	10	—
<i>Astragalus purshii</i>	60	0.5	<i>Eriogonum microthecum</i>		
<i>Astragalus iodanthus</i>	30	0.3	var. <i>lapidicola</i>	10	—
<i>Phlox stansburyi</i>	30	0.1	<i>Eriogonum umbellatum</i>		
<i>Cymopterus watsoni</i>	20	0.1	var. <i>juniporinum</i>	10	—
<i>Erigeron caespitosus</i>	20	0.2	<i>Ribes velutinum</i>	10	—
<i>Lomatium macrocarpum</i>	20	0.4			
<i>Lomatium nevadense</i>	20	—	Annual forbs		
<i>Lupinus</i> sp.	20	—	<i>Gilia brecciarum</i>	80	11.8
<i>Senecio multilobatus</i>	20	0.1	<i>Collinsia parviflora</i>	70	7.7
<i>Agoseris glauca</i>	10	0.1	<i>Cryptantha watsonii</i>	60	0.9
<i>Allium atrorubens</i>	10	0.1	<i>Gayophytum ramosissimum</i>	60	3.7
<i>Antennaria rosea</i>	10	—	<i>Microsteris gracilis</i>	60	11.9
<i>Arenaria kingii</i>	10	—	<i>Mentzelia albicaulis</i>	50	0.5
<i>Astragalus</i> sp.	10	—	<i>Eriastrum sparsiflorum</i>	50	0.1
<i>Astragalus calysosus</i>	10	—	<i>Polygonum douglasii</i>	50	0.5
<i>Astragalus filipes</i>	10	—	<i>Gayophytum nuttallii</i>	40	0.8
<i>Calochortus nuttallii</i>	10	—	<i>Gilia tennerrima</i>	40	3.2
<i>Comandra pallida</i>	10	—	<i>Gilia violaceum</i>	30	0.9
<i>Cordylanthus kingii</i>	10	—	<i>Cryptantha torreyana</i>	30	0.7
<i>Crepis occidentalis</i>	10	—	<i>Descurainia richardsonii</i>	30	0.1
<i>Cryptantha flavoculata</i>	10	0.2	<i>Linanthus septentrionalis</i>	30	0.6
<i>Erigeron argentatus</i>	10	—	<i>Navarretia breweri</i>	30	0.1
<i>Haplopappus acaulis</i>	10	—	<i>Chenopodium album</i>	10	—
<i>Ipomopsis congesta</i>	10	0.1	<i>Calytonia perfoliata</i>	10	—
<i>Lithophragma bulbifera</i>	10	—	<i>Collomia grandiflora</i>	10	—
<i>Pedicularis crenulata</i>	10	—	<i>Epilobium paniculatum</i>	10	—
<i>Penstemon eatoni</i>	10	—	<i>Erigonum vinineum</i>	10	—
<i>Penstemon kingii</i>	10	—	<i>Galium bifolium</i>	10	—
<i>Penstemon speciosus</i>	10	0.5	<i>Phacelia affinis</i>	10	—
<i>Streptanthus cordatus</i>	10	—	<i>Phacelia humilis</i>	10	5.2

¹Species nomenclature from Holmgren and Reveal (1966).
²Constancy: number of stands where species occurs/total number of stands.
³Importance values: species total percent cover × constancy. Relative importance value (RIV): (species importance value/max importance values)×100.
⁴RIV <0.1 not shown.

Individual species cover within the understory was so sporadic that species data had to be combined and transformed ($\log [x + 1]$ or $\arcsine \sqrt{\%}$) to effectively reduce skewness and kurtosis. Plant data were grouped into totals for perennial and annual species before running in a two-way factorial analysis with the second factor, soil microsites (duff, transition, interspace). Data from each site were analyzed separately, using transects as replicates. Differences in the proportion of total plant cover and plant cover/m² of microsite between duff and transition soil microsites and between their mean value and that of interspace were compared in a series of completely orthogonal contrasts. Orthogonal contrasts are generally viewed as stronger statistical tests than the more commonly used multiple range tests, but are limited in that fewer treatments can be tested and all treatments tested must be orthogonal to each other. Proportion of total plant cover by soil microsite was used to show distribution of plant cover among microsites without compensating for differences in area. Plant cover/m² was used to show relative "favorableness" of a microsite for understory on a per unit basis.

RESULTS AND DISCUSSION

STAND CHARACTERIZATION.—The junior author identified a total of 73 understory taxa in the sampled stands (Table 1). As our study was limited to only pinyon-juniper stands in late succession stages and correspondingly high tree cover (Table 2), we found fewer understory species than previously reported for pinyon-juniper woodland of the Great Basin (Tueller et al. 1979). Rabbitbrush (*Chrysothamnus* sp.) species were notably absent from our sites, but annual forbs, little blue-eyed Mary's (*Collinsia parviflora*), borage

(*Cryptantha* sp.), and the perennial grass, Sandberg bluegrass, had much higher constancy values than were previously reported by the above authors. We tentatively suggest rabbitbrush disappears more rapidly than other shrubs as pinyon-juniper competition increases, and annual forbs increase. Long-term successional studies are required to test this idea.

Perennial forbs had the greatest number of species (31) among stands. Next in order were annual forbs (23), shrubs (11), perennial grass (7), and annual grass (1) (Table 1). Although perennial forb species were numerous, they were not ubiquitous. Only 32 percent of the perennial forbs were found on more than one stand, as compared with 70 percent of the annual forbs, 73 percent of the shrubs, and 57 percent of the perennial grass. The range of constancy values, 10–90 percent (Table 1), reflect the variability in individual species occurrence among stands. The annual forb plant form class had the greatest number of species with ≥ 50 percent constancy values.

A relative importance value (RIV) was used to indicate the relative importance of a species in providing understory cover in sampled stands (Table 1).

Importance value (IV)

= constance • percent cover (sum of all stands)

Relative importance value (RIV)

= (species IV / max IV [all species]) • 100

We found important understory species ($RIV \geq 5$) to be Sandberg bluegrass, squirrel-tail (*Sitanion hystrix*), phlox (*Phlox hoodii*), big sagebrush (*Artemisia tridentata*), microsteris (*Microsteris gracilis*), gilia (*Gilia brecciarum*), blue-eyed Mary's, phacelia (*Phacelia humilis*).

TABLE 2. Percent tree cover on the 10 study sites.

	Study site									
	Mt. Wilson	Monitor	Fred-ricks	House Canyon	Willow Creek	Camel Springs ¹	Ridge ¹	Paper-back	Austin	Lowry Springs
Tree species:										
<i>Pinus monophylla</i>	52	63	36	13.4	38	58	52	56	29	30
<i>Juniperus osteosperma</i>	4			12.3	3				14	20
Total cover	56	63	36	25.7	41	58	52	56	43	50

¹Cover values from Meeuwig (1979).

TABLE 3. Number of species by plant group.

Plant form	Site										\bar{x}	CV ¹
	Mt. Wilson	Monitor	Fredricks	House Canyon	Willow Creek	Camel Springs	Ridge	Paper-back	Austin	Lowry Springs		
Shrubs	0	1	2	4	5	3	3	3	3	4	2.8	(%) 50
Perennial												
Grass	1	2	2	2	3	2	2	3	2	6	2.5	51
Forb	2	1	0	8	6	2	5	6	6	18	5.4	90
Annual												
Grass	1	0	1	0	0	1	1	1	0	0	0.5	100
Forb	3	8	12	9	8	10	10	15	8	2	8.5	43
Total	7	12	17	23	22	18	21	28	19	30	19.7	33

¹CV (%): coefficient of variation = $\left(\frac{\text{Standard deviation}}{\text{Mean}} \right) \times 100$.

Sandberg bluegrass was by far the most important structural component of the understory. All perennial forbs had low relative importance values because of low cover values.

Number of understory species occurring on a single site varied from seven to 30 among sites with a mean of approximately 20 species (Table 3). Total number of understory species at each site varied less (coefficient of variation [CV] = 33 percent) than species numbers in individual plant groups among stands (Table 3). At least four plant groups were represented at each stand. Annual forbs had the greatest number of species on all sites except Lowry Springs. Annual forbs also had the least variability of the plant forms in species numbers among stands (CV = 43 percent). The predominance of annual species is characteristic of pinyon-juniper woodlands here and in New Mexico, but in Utah perennial forbs predominate (Harner and Harper 1976) (Table 4). Low variability in the relatively large number of annual forb species among stands indicate annual forbs have adapted to utilize the limited resources available within fully stocked stands; but because

of the ephemeral nature of annuals they utilize these resources on an intermittent basis. A diversity of plant groups at each stand also suggested that, although limited, resources available under the intense tree competition can still meet the demands of physiologically different species.

Understory cover was low (\bar{x} = 3.4 percent) with a high coefficient of variation (CV = 60 percent) among stands (Table 5). Cover values ranged from 0.02 percent at Mt. Wilson to 7.19 percent at Fredricks. These values are low, but are probably an overestimate of "normal" understory cover; 1978 was a wetter year than "average" on many sites. St. Andre et al. (1965) reported similar low cover values (\bar{x} = 2.65 percent) for herbaceous understory in the pinyon woodland of the White Mountains in California.

No one plant form class had the greatest proportion of cover on all sampled stands, but annual forbs and perennial grass consistently made up a large portion of the understory cover (Table 5). There were high coefficients of variation in the proportion (p) of total plant cover for plant group classes

TABLE 4. Mean percent of species contributed by plant group.

	Shrub	Perennial		Annual	
		Grass	Forb	Grass	Forb
Nevada	14.2	12.6	27.4	2.7	43.1
Utah ¹	18.8	17.0	39.8	24.4	
New Mexico ¹	24.9	13.5	24.4	37.2	

¹From Harner and Harper (1976).

among stands, but less variation among annual forb and perennial grass classes. Results suggest that the perennial grass, Sandberg bluegrass, and annual forbs are well adapted to coexist within fully stocked pinyon and juniper stands.

SOIL MICROSITES AND PLANT GROWTH.—

The duff microsite occurred more often in transects and correspondingly occupied a greater proportion of the ground surface than the transition microsite on all stands (Table 6). Contrary to expectations, the proportion of understory on the transition microsites exceeded that of duff on five of nine sites tested (Table 7). This anomaly and lack of significant differences in the proportion of understory cover between duff and transition microsites on seven of nine sites suggests both microsites provide a similar amount of understory cover, but cover provided by transition microsites is disproportionately greater than the surface area it occupies.

This supposition was substantiated by greater plant cover/m² (Table 8) in transition than duff microsites in tree-to-tree transects in seven of the nine sites. This relationship was significant at Austin, Willow Creek, Ridge, Paperback, and Monitor. Only at Fredricks, where duff was shallow and the understory dominated by the annual forb *phacelia* (*Phacelia humilis*), did duff plant cover/m² significantly exceed that of transition microsites. The close association of *Pha-*

celia vallismortae with pinyon trees has been previously reported by St. Andre et al. (1965).

The completely orthogonal contrast procedure prohibited the direct comparison of plant cover on transition and interspace microsites, but transition microsites had greater proportion of total plant cover and greater plant cover/m² than interspace at seven of nine sites as indicated by values in Tables 7 and 8. Differences in plant cover/m² between transition and interspace indicate the favorableness of the transition microsite for understory growth and are not the result of differences in numbers of each microsite sampled.

Duff and transition microsites combined exceeded interspace in total number and corresponding surface area in all stands except Willow Creek and House Canyon (Table 6). The total proportion of plant cover provided by duff plus transition microsites greatly exceeded the proportion of plant cover on interspace microsites at all stands but Willow Creek and Lowry Springs (Table 7).

We could not determine significant differences ($p \geq 0.1$) in proportion of understory cover between interspace microsites and the mean of tree-associated microsites (duff + transition/2) at six of nine stands (Table 7). At Fredricks and Paperback mean understory cover on tree-associated microsites was significantly greater than the interspace, but the

TABLE 5. Proportion (π) of total plant cover by plant group class and total plant cover (%) among stands.¹

Site	Shrub π (%) ²	Perennials		Annuals		Total plant cover (%) ³
		Grass π (%)	Forb π (%)	Grass π (%)	Forb π (%)	
Mt. Wilson	—	4.2	4.2	4.2	87.5	0.02
Fredricks	—	—	—	—	100.0	7.18
House Canyon	17.6	9.7	4.6	—	68.1	1.64
Willow Creek	95.8	0.7	0.1	—	3.4	4.44
Camel Springs	29.9	36.7	4.1	—	29.3	3.38
Paperback	18.8	49.1	2.1	6.1	23.9	5.58
Monitor	2.9	71.6	2.1	—	23.3	1.39
Austin	0.8	74.5	4.0	—	20.7	2.46
Ridge	5.2	83.0	1.3	0.4	10.1	4.92
Lowry Springs	9.0	53.7	37.2	—	—	3.11
\bar{x}	18.0	38.3	6.0	1.1	36.6	3.42
CV (%) ⁴	153	81	176	194	92	60

¹Data from the five parallel transects.

²Proportion (π) of the total plant cover provided by each plant form in percent.

³Percent cover: total plant cover as percent of ground surface it covers.

⁴CV (%): coefficient of variation = $\left(\frac{\text{Standard deviation}}{\text{Mean}} \right) \times 100$.

TABLE 6. Number of frames¹ identified as duff, transition, or interspace microsites.²

Microsite	Site									
	Mt. Wilson ³	Monitor	Fredricks	House Canyon	Willow Creek	Camel Springs	Ridge	Paperback	Austin	Lowry Springs
Duff (D)	33 (55)	43	52	34	31	44	54	46	57	53
Transition (T)	18 (30)	42	24	15	11	30	28	27	16	20
Interspace (I)	9 (15)	15	24	51	58	26	18	27	27	27

¹Number of frames equates to percent ground surface occupied by the microsite.
²Data from the five parallel site transects (100 total frames).
³Two transects at Mt. Wilson were deemed unusable due to large differences in tree ages from the major portion of the stand; thus percent ground surface occupied by each microsite is in parentheses.

opposite occurred at Willow Creek. Cover differences are due to microsite “favorableness” at Fredricks, as indicated by greater plant cover/m² on tree-associated microsites (Table 8). At Willow Creek and Paperback differences in proportion of plant cover are due to differences in surface areas of the microsites.

The lack of significant differences in proportion of plant cover and plant cover/m² on tree-associated microsites versus interspace suggests overall favorableness of tree-associated microsites is not different from that of interspace on most sites. The presence of tree root competition in all microsite types of fully stocked stands (Woodbury 1947 and our own observations) would tend to lower production on all microsites and ameliorate differences. This hypothesis is in variance with previous reports of increasing understory production under tree crowns of alligator juniper (*Juniperus deppeana*) (Clary and Morrison 1973) and apparently an increase in production with distance from the stem of one-seeded juniper (*Juniperus monosperma*) (Arnold 1964).

PERENNIAL AND ANNUAL PLANT COVER.—Proportion of understory cover provided by

annuals and perennials varied greatly among stands. Understory at Mt. Wilson, Fredricks, and House Canyon was dominated by annual forbs, but perennials (shrubs and grass) dominated the understory on the remaining stands (Table 7). Both annuals and perennials are adapted to coexist with the overstory species. The majority of species (excluding shrubs), either perennial or annual, complete growth early in the growing season before surface soils become dry (unpublished data).

INDIVIDUAL SPECIES.—Sandberg bluegrass was found to have greater cover in transition microsites than duff or interspace on five stands where it dominated the understory (data not shown). Plant density was also greater in the transition microsite, but not significantly so. Arizona fescue (*Festuca arizonica*) was reported to have a similar distribution pattern in a pinyon-juniper community in Arizona (Merkle 1952).

Other understory species occurred too infrequently within individual frames to be analyzed parametrically, but did appear to favor one microsite over another. *Cryptantha* species occurred more often in the duff microsites than elsewhere.

TABLE 7. Orthogonal comparisons of the proportion of total understory cover among soil microsites and perennial and annual species.¹

Orthogonal comparisons	Site									
	Mt. Wilson ²	Monitor	Fredricks	House Canyon	Willow Creek	Camel Springs	Ridge	Paperback	Austin	Lowry Springs
D vs T ³ ($\frac{D+T}{2}$)	—	16:64 ⁴	72:21	44:17	2:16	31:54	46:34	33:48	40:28	22:27
versus I	—	40:20	46:7	30:39	9:82	42:15	40:20	40:19	34:32	24:51
Perennials versus annuals	—	75:15	0:99 [*]	32:68	96:04	70:30	89:11	72:28	77:23	100 [*] :00

¹Plant cover from the five parallel transects at each site.
²Understory cover at the Mt. Wilson site was so sparse as to prohibit parametric analysis.
³D = duff microsite, T = transition microsite, I = interspace microsite.
⁴—, —, denotes significant difference at 0.05 and 0.1 levels, * a biologically significant difference is assumed without statistical testing.

CONCLUSIONS

Numerous species and plant groups occur in the understory of fully stocked stands of pinyon and juniper, but numbers of species on any one stand are moderately low (\bar{x} = 20) and they provide scant cover (\bar{x} = ≤ 5 percent). A perennial grass, Sandberg bluegrass, and several annual forbs consistently provided the most understory cover among stands. Consistency in cover and a high number of species among stands indicated the annual forb plant group may be best adapted to coexist with the overstory species in fully stocked stands. The ephemeral nature of the annual forbs increases the year-to-year variability in understory cover and decreases the predictability of response if woodlands are disturbed. Management operations that remove tree cover should consider the scant understory in most stands and the potential erosion hazards.

Plant cover decreases in both directions from the transition microsite; thus response is at variance to previous reports of both decreasing and increasing cover toward the stem of pygmy forest tree species. The proportion of understory cover on duff and transition microsites is similar in most stands. Although duff occupied greater surface area, the transition microsite produced greater plant cover/m². Transition microsites appear more favorable for growth of understory species than those of duff or interspace. Tree-associated microsites provide more understory cover than interspace because they occupy a larger portion of the stand; they do not increase understory cover over that which could be expected from interspace.

Land managers should recognize that fully stocked pinyon-juniper woodlands are a com-

posite of soil microsites that contain different proportions of the understory cover. These microsites may well respond differently to management practices; thus understory production will vary under the same management when proportions of the microsites vary.

ACKNOWLEDGMENT

We thank reviewers Neil E. West, A. Winward, P. T. Tueller, and Kimball Harper for their comments. Assistance with field work by Clay Gautier, JoAnne Potter, and Lynda Peck is greatly appreciated.

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TABLE 8. Orthogonal comparison of the mean plant cover (dm²/m² occurring on each soil microsite.¹

Orthogonal comparisons	Site									
	Mt. Wilson ²	Monitor	Fred-ricks	House Canyon	Willow Creek	Camel Springs	Ridge	Paper-back	Austin	Lowry Springs
D vs T ³		0.3:2.3 ⁴	10.3:5.4	3.2:3.1	0.6:7.4	1.6:4.6	2.8:8.5	3.7:8.3	0.8:4.7	2.2:3.7
($\frac{D+T}{2}$) vs I	—	1.3:2.4	7.9:1.2	3.1:2.9	4.0:4.1	3.1:2.1	5.7:6.8	6.0:5.6	2.8:7.6	3.0:1.5

¹Plant cover based on data from tree-to-tree transects.

²Understory cover at Mt. Wilson site.

³D = duff microsite; T = transition microsite; I = interspace microsite.

⁴—, — denotes significant difference at 0.05 and 0.1 levels.

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ASSOCIATION OF RHABDOCLINE NEEDLE BLIGHT AND EPICORMIC BRANCHING IN DOUGLAS-FIR

Ronald M. Lanner¹ and James A. Bryan¹

ABSTRACT.— In northern Utah, Douglas-firs (*Pseudotsuga menziesii* [Mirb.] Franco) with symptoms of *Rhabdocline* needle blight had a significantly higher frequency of epicormic branching than did healthy trees. It is not known whether *Rhabdocline* infection stimulates epicormy, or whether the proliferation of epicormics increases resistance to the disease.

Rhabdocline needle blight is a leaf disease of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) caused by the ascomycete *Rhabdocline pseudotsugae* Syd. (Hepting 1971). Infection sometimes results in defoliation serious enough to cause death, even in relatively vigorous trees up to 100 years old (Davidson and Prentice 1967).

Douglas-fir, especially in the Rocky Mountains, is subject to the formation of epicormic branches that arise from dormant buds borne at the base of primary branches. The occurrence of epicormics appears to be a normal consequence of branch decline not requiring pest attack for its expression (Bryan and Lanner 1981), but the added stress of *Rhabdocline* defoliation may increase the frequency of epicormics in infected trees. The purpose of the observations reported here was to determine whether trees infected by *Rhabdocline* differ from healthy trees in their frequency of epicormic branches.

METHODS

These observations accompanied a detailed morphological study of epicormics that has been reported elsewhere (Bryan and Lanner 1981). Pole-sized Douglas-firs were selected at intervals along trails in Logan Canyon, Cache National Forest, Utah. *Rhabdocline*-infected trees were identified by the sparseness of their crowns, which had lost many of the needles predating those of the current year (N. Van Alfen, pers. comm.). These trees were found mainly in dense, pure stands on north-facing slopes between 1524 and 1860

m elevation, and often near streams. Uninfected trees in those stands were chosen randomly for comparison. Trees were examined in the summer, when needles infected in the previous year had already fallen (Davidson and Prentice 1967). Epicormic frequency was determined by examining the 10 uppermost dead primary branches below the base of the live crowns, and recording the number of those branches with associated epicormics. The Z-test (Dixon and Massey 1969) was used to test the hypothesis that the mean number of epicormics was equal for healthy and diseased trees. The hypothesis that the frequency distributions were equal was tested with the Kolmogorov-Smirnov two-sample test (Conover 1971).

RESULTS

Trees with *Rhabdocline* symptoms had an average of 4.8 (of 10) branches with epicormics in the lower crown, but similar healthy trees averaged only 3.0 such branches (Table 1). The Z-value of 2.23 was significant at the 99 percent level. The frequency distribution of trees with n number of epicormics also differed significantly ($\alpha = .05$) between healthy and diseased trees (Table 2).

DISCUSSION

It is apparent that *Rhabdocline*-infected trees exhibit a higher frequency of epicormics than do healthy trees. Our data do not indicate whether this is because repeated or periodic defoliations stimulate epicormic

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formation, or whether trees that are *Rhabdo-*
cline-susceptible also happen to be prone to
epicormics. A third possibility is that suscep-
tible trees are more likely to survive *Rhabdo-*
cline if they balance their losses of photo-
synthetic surface area with new foliage borne
on epicormic branches. If this is the case,
Rhabdocline-infected trees incapable of pro-
ducing numerous epicormics may have
evaded our sample by suffering higher morta-
lity. Douglas-firs in Logan Canyon, as else-
where, show marked individual variability in
their production of epicormics (Bryan and
Lanner 1981).

Johnson and Denton (1975) have credited
epicormics with promoting the survival of
Douglas-firs partially defoliated by the
spruce budworm. The survival of trees in-
fected by *Rhabdocline* might also be pro-
moted by epicormics. *Rhabdocline*-infected
trees may repeatedly cast off all their one-
year-old foliage the year following infection,
thus suffering a heavy loss of photosynthetic
surface. Epicormics stimulated by the in-
creased solar radiation permitted by such de-
foliation may serve as an important source of
needed photosynthate. If the sprouting of
epicormics indeed enables Douglas-fir to re-
cover from *Rhabdocline* and extend its repro-
ductive life, we would expect natural selec-
tion to result in a higher frequency of that
trait where *Rhabdocline* is of high frequency.
According to Hepting (1971), Rocky Moun-
tain Douglas-fir (var. *glauca*) is extremely sus-
ceptible to *Rhabdocline* but the Pacific coast
variety (var. *menziesii*) is relatively resistant.
Our studies (Bryan and Lanner 1981) show
that in the eastern part of the intermountain
area nearly all the Douglas-firs produce epi-
cormics, but in the western part of this re-
gion epicormic production is extremely vari-
able and is even exceeded by epicormic

TABLE 1. Number of branches with epicormics on
Douglas-fir trees in Logan Canyon, Utah, in relation to
Rhabdocline infection.¹

<i>Rhabdocline</i> condition	Number of branches of 10		
	Mean	Range	S.D.
Healthy trees (n = 73)	3.0a	0-10	2.5
Infected trees (n = 20)	4.8a	0-8	2.9

¹Values followed by the same letter differ significantly at 0.01 level.

frequency in coast Douglas-fir. Thus, central
Idaho plots had considerably fewer trees with
epicormics than the average of several Cali-
fornia plots, and the range was also far lower.
Therefore, unless it is demonstrated that
Rhabdocline is a more serious pest of
Douglas-fir in the eastern intermountain re-
gion than in Idaho, our results do not support
the hypothesis that *Rhabdocline* has been a
significant factor, at least at the regional lev-
el, in selection for epicormic branching. Fur-
ther study of the role of epicormics in
Douglas-fir survival and longevity seems war-
ranted, whether or not it bears a relationship
to *Rhabdocline* resistance.

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TABLE 2. Frequency distribution of epicormic
branches on healthy and *Rhabdocline*-infected trees.¹

Number of lateral branches with associated epicormics	Healthy trees	Diseased trees
	Percent of total	
0	15.1	4.3
1	17.8	17.4
2	15.0	8.7
3	16.5	8.7
4	12.3	8.7
5	12.3	8.7
6	1.4	13.1
7	0	17.4
8	2.7	13.0
9	5.4	0
10	1.4	0

¹Based on observations of 10 branches per tree on 73 healthy trees and 20
Rhabdocline-infected trees.

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